University of Alberta

Response of small mammals to landscape structure at multiple spatial scales

by

Cristine V. Corkum

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

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This thesis is dedicated, in loving memory, to my grandfather

Charles A. Corkum.

Abstract

This study examined spatial, temporal and scalar variation in *Clethrionomys gapperi* (red-backed voles) and *Peromyscus maniculatus* (deer mice) response to landscape structure in mixed-wood boreal forests of northeastern Alberta. Relative abundance was estimated by live-trapping on systematic grids during spring and fall. Landscape structure was defined by composition (amounts) and spatial configuration (arrangement) of forest stand and understory patch types at different extents around grid points and related to species abundance by generalized linear models. *Clethrionomys gapperi* responded to landscape at a stand level at all extents, but configuration effects were limited to fall on grids where marginal habitat was abundant. *Peromyscus maniculatus* responded strongly only to forest stand composition, also in fall on grids with abundant low-quality habitat at all extents. No species responded consistently to understory patch configuration, but composition was important and associations changed with landscape extent, indicating foraging requirements at small extents and dispersal associations at larger extents.

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Chapter 1 - General introduction

A landscape is a terrestrial area that is perceived as a mosaic of different land elements (Forman 1997), each varying in quality or function for a species present. Landscape ecology is the study of how organisms interact with the landscape where they live or travel. Dunning *et al.* (1992) outlined four ways in which organisms interact with landscapes. These include landscape complementation and supplementation, source/sink dynamics and neighbourhood effects. Landscape complementation is the mandatory use of more than one landscape element, or patch type, during an individual's lifetime. Landscape supplementation is similar in that small habitat patches may be occupied only when other patches in the landscape supplement resources. Source/sink relationships that determine population size in patchy populations occur where habitat quality varies across landscapes. And neighbourhood, or boundary, effects result from interspecific interactions, microclimate changes and dispersal barriers at the borders of neighbouring patches in landscapes.

Landscape structure has been investigated as a driver of spatial population patterns in recent years due to increasing landscape fragmentation by human expansion and to biologists' growing access to remotely sensed vegetation information and digital mapping techniques. There are a number of measurable landscape features that are likely to determine landscape effects on large-scale processes during which species interact with landscape structure. Fahrig and Merriam (1994) review these for the process of dispersal, which they conclude is probably the most important process to consider in relation to landscape structure. The landscape structural features which may affect dispersal, and thus local population size and stability, include patch size, shape and quality, dispersal route availability and quality, and spatial configuration of components. Smaller, more isolated patches tend to support less stable populations due to increased extinction rates and decreased immigration (Levins 1970, Smith 1974, van Apeldoorn *et al* 1992, Kozakiewicz and Gortat 1994). Patches with more complex shapes contain more edge habitat relative to interior. Edge habitat may be very different from the abutting habitat interiors if there is a large degree of contrast between them in terms of vegetation (Voller 1998). This may result in differences in plant and animal species composition and interspecific interactions (Forman 1997). Dispersal routes such as corridors enhance connectivity between habitat patches and alleviate effects of small patch size and large isolation by distance (Wegner and Merriam

1979, Fahrig and Merriam 1994). Connectivity is also determined by the quality of non-habitat patches in the matrix for movement (Taylor *et al.* 1993). Spatial configuration of patches is important in that it determines the degree of isolation of different patch types, as well as the connectivity between them and the types of edges or boundaries that will be present.

The ability of researchers to detect landscape effects on populations is determined by the spatial scale at which landscapes are measured. When choosing a scale to study, one must decide a grain and extent of the landscape with which to work. Grain refers to the smallest patch size a species is likely to perceive while extent is simply the overall size of the landscape to which that species responds (Kotliar and Weins 1990). Patches are usually defined as internally homogeneous entities, but a hierarchical model of patch structure should be recognized when defining a spatial scale for study (Kotliar and Weins 1990). Though a patch is homogeneous at one scale, examination at finer and coarser resolutions reveals patches within patches. A single species may respond to more than one of these levels of patchiness or to different landscape extents, depending on the spatial scale of the process causing the response (Weins 1989, Collins and Glenn 1997). When one knows the spatial scale of the process of interest, quantifying landscape structure for study is a fairly easy task, as long as maps of the landscapes are available at the necessary scales. However, it is usually rare to have this much detail about a species' response to patchiness, so it has been suggested that landscape ecologists take a multi-scale approach to studying landscape effects (Collins and Glenn 1997, Roland and Taylor 1997).

The following study examines the effects of landscape structure on two small mammal species in the mixed-wood boreal forest of northeastern Alberta: red-backed voles, *Clethrionomys gapperi*, and deer mice, *Peromyscus maniculatus*. Forests in this region are naturally heterogeneous, with a number of different stand types visible in aerial photos. Photo interpretation is used to produce land cover maps for the region, called the Alberta Vegetation Index, which is useful for landscape ecology work. Patch boundaries on these maps were redefined for this study to better approximate stand-level patchiness perceived by the small mammals, and species abundance at a number of points was related to surrounding stand-level landscape structure. A subset of these landscapes was also mapped by patches at a much smaller grain of understory vegetation, with the smallest patches only 5- by 5-m in

size. In both analyses, the extent of landscapes considered was varied to approximate landscape sizes relevant to the processes of dispersal and foraging.

The goals of this multi-scale approach were to increase the probability of using the correct spatial scale(s) of response for these species and to compare the magnitude to which landscape structure affects different spatial processes (distinguished from each other by shifts in response across scales). Results will add to the current knowledge of habitat associations for these species, at spatial scales and contexts that have not been previously investigated. Conclusions from this work will also be incorporated into a larger integrative project within the framework of the Sustainable Forestry Management Network (SFMN, a large network of research centres conducting similar work on these and other species throughout Canada). Scalar differences in response to landscape may be related to species characteristics such as body size, dispersal capabilities and resource requirements, or to regional differences in landscape context. These and other data from SFMN projects may help to reveal trends in organismal scaling (Collins and Glenn 1997), so that appropriate scales of landscape research may be more closely approximated in future work. Conclusions are also expected to be of use to land managers when creating landscape-scale harvest plans in the mixed-wood boreal forest that minimize impacts on wildlife and ecosystem function.

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Chapter 2 - Effects of stand-level landscape structure on small mammal abundance

Introduction

Past research has shown that local presence and abundance of many mobile animal species is influenced by the structure (composition and configuration) of surrounding landscapes (Weins *et al.* 1993). Landscape composition refers to the overall amount of different patch types in a landscape, while configuration describes the physical arrangement of these patches in space (McGarigal and Marks 1994). These concepts are important in understanding population spatial distributions because composition may indicate a landscape's potential to provide immigrants to a point in space or resources to residents at that point, whereas configuration affects a landscape's permeability to movement (Fahrig and Merriam 1994). Source/sink (Pulliam and Danielson 1991) and metapopulation (Levins 1970) dynamics, as well as island biogeography theory (MacArthur and Wilson 1967), form the foundations of landscape ecology. All of these theories incorporate movement patterns of individuals among isolated local populations and imply its importance for population persistence in fragmented systems. Landscape permeability and connectivity, products of both composition and configuration, affect the probability of individual movement among habitat patches (Kozakiewicz 1993, Taylor *et al.* 1993) and hence are of interest to ecologists.

Both the availability of dispersers in a population, and the distances they travel, are important factors controlling the magnitude of landscape effects on species distributions (Fahrig and Paloheimo 1988a, Bowers and Dooley 1991, Szacki *et al.* 1993, Fahrig and Merriam 1994). Tellaria and Virgós (1997) showed that distance from source habitat (a measure of connectivity) limited roe deer distributions in fragmented landscapes in central Spain. Mönkkönen *et al.* (1997) showed that the amount of open habitat (a potential barrier to dispersal) at large spatial scales was negatively associated with flying squirrel presence in local patches of usable softwood, likely due to inhibition of movement to these patches. Fahrig and Merriam (1985) demonstrated the importance of landscape connectivity in white-footed mice, *Peromyscus leucopus*, where overwinter extinctions occurred in isolated forest patches due to lower recruitment via immigration. These are but a few examples where

landscape structure has been associated with species distributions and population persistence due to impacts on movement.

In addition to affecting the probability of occupation of a point in space, landscape structure at smaller extents (areas) influences the probability of individuals staying in that place. Elements of surrounding landscapes may serve as supplementary habitat for animals occupying marginal habitat, making it more hospitable than it may otherwise have been (Dunning *et al.* 1992). Spatial structure of resource patches may also have direct effects on habitat quality within a home range, as shown in a number of multi-scale studies. In the Finnish study on flying squirrels, it was demonstrated that landscape extents approximating home range areas around squirrel nests had relatively more softwood (resource) area than random sites (Mönkkönen *et al.* 1997). Grubb *et al.* (1997) and Ripple *et al.* (1997) both conducted analyses of landscape structure within spotted owl home ranges and also demonstrated differences in stand-level landscape composition surrounding nest sites versus random sites. These observations may not seem surprising and some may argue are not landscape effects at all. However, they do represent a different approach to measuring home range quality that looks beyond microhabitat, within-patch associations to consider structure of available habitat types at larger scales that are typically easier for humans to measure and manage.

Landscape associations seen at the scale of home ranges may change or disappear when landscapes of larger or smaller sizes are investigated (Grubb *et al.* 1997, Mönkkönen *et al.* 1997), indicating that landscape structure is assessed by animals at different spatial scales for different purposes. This is consistent with current theory in landscape ecology (Weins 1989, Collins and Glenn 1997). Response to landscape structure may be most prominent during particular stages of an animal's life history (*i.e.* during the dispersal phase) or act at different spatial scales depending on characteristics of the species concerned (*i.e* Holling 1992, Milne *et al.* 1992) and the process that is being affected (Bowers and Dooley 1991, Morris 1992).

This study examines spatial, temporal and scalar variation in small mammal response to landscape structure in the mixed-wood boreal forest of northeastern Alberta, Canada. The analysis is unique in that it isolates landscape effects from those of local vegetation (within a single habitat patch) and spatial coordinates. It also separates the effects of landscape composition and configuration, which are sometimes difficult to discriminate.

Local vegetation is expected to influence abundance of small mammals, as this often dictates the availability of food and shelter in an area. However, the habitat type of a point (as measured by vegetation characteristics) is often correlated with landscape structure around that point. Because of this correlation, local habitat effects should be accounted for in any study of landscape effects. Spatial structure of populations (as measured by geographic coordinates), results in spatial autocorrelation at certain scales, such that there is non-random similarity or dissimilarity of proximate points in space (Legendre 1993). Population spatial structure may covary with landscape structure and habitat when sampling over large areas. This requires the consideration of spatial position of samples in landscape ecology studies to identify the amount of spatial variation in species abundance that exists independently of landscape and local habitat effects.

The boreal mixed-wood forest in northeastern Alberta provides landscape forms in which landscape ecology studies have not traditionally been conducted. Past research has typically been conducted in highly fragmented landscapes such as agricultural landscapes, with a high degree of contrast between usable habitat patches and suboptimal matrix habitat. The boreal forest is also heterogeneous, containing a number of different forest stand types existing in a variety of sizes, shapes and successional stages. But patterns there are due to topography, moisture regimes and naturally occurring large-scale forest fires. Contrast between disturbed and undisturbed forest is less distinct due to the rapid regeneration of aspen (*Populus* sp.). In the recent past, logging of mature aspen stands for pulp production has increased in Alberta, providing another source of change in landscape structure. Both fire and harvesting remove relatively large patches of canopy trees, causing microclimate changes on the forest floor (Carleton and MacLellan 1994). However, fire disturbance tends to be more erratic, forming large, irregularly-shaped patches of young forest, whereas harvesting generally creates smaller, simpler shapes and selectively removes merchantable timber of particular age classes. Succession post-disturbance is also different between burned and harvested stands due to the volume of standing dead trees and the abundance of seeds available for regeneration after burning (Carleton and MacLellan 1994). However, pre-disturbance forest type may mediate this difference since trees in aspen forests experience rapid regeneration in the absence of snags. This study offers the opportunity to contrast landscape effects in a region where heterogeneity is an historic condition and where different types of disturbance are presently creating structure.

This study measured distribution and abundance of animals over very large areas, encompassing a wide variation in forest landscape structure, thereby increasing the ability to detect responses to landscapes defined by canopy cover of forest stands. However, these large scales limit the types of fauna one may examine. Two small rodents, *Clethrionomys gapperi* (the red-backed vole) and *Peromyscus maniculatus* (the deer mouse), were chosen for this study. These species are common, but exhibit spatial variation in abundance that remains largely unexplained by studies to date. Both species are small and easily trapped, with movement abilities and home range area requirements that correspond to the landscape scales that are logistically feasible. Life history characteristics of *C. gapperi* and *P. maniculatus* make them useful for studying changes in landscape effects during different ecological processes by examining distributions in different seasons. In northeastern Alberta, both species breed from mid-May to mid-September (personal observations). Many rodent species with seasonal reproduction experience dispersal during the summer months when populations are increasing (*e.g.* Krebs *et al* 1976, Bondrup-Nielsen and Karlsson 1985). For both species then, we may assume that spring distribution reflects processes like foraging and home range selection because these likely determine overwinter survival (Karlsson 1997), whereas fall distribution results from recruitment due to local reproduction and larger scale processes like dispersal and migration.

A number of recent studies in landscape ecology have identified the need for multiple scale research due to the limited knowledge of effects at different scales (Collins and Green 1997, Roland and Taylor 1997). This lack of information makes it difficult to correctly estimate the appropriate sampling scale for experiments *a priori*. Therefore, point sampling in this study was conducted on grids at two spatial scales, varying both grain (point spacing) and extent (grid size). The area of landscapes considered around sampling points was also varied to determine what landscape size has the greatest effect on small mammal abundance. Different movement behaviours based on species and season may cause landscape effects to occur at different spatial scales.

Considering all of these sources of variation (landscape composition and configuration, local vegetation, spatial structure, study area, season, sampling scale and landscape extent), three questions will be addressed for each species. Each question may be associated with a number of hypotheses and predictions that are outlined in Table 2-1.

Question 1: What are the effects of landscape configuration and composition on small mammal abundance in the mixed-wood boreal forest after controlling for local vegetation effects and inherent population spatial structure?

Question 2: How does the magnitude of effects of four explanatory components (landscape configuration, landscape composition, local vegetation, and spatial position) change with study area, season and sampling scale?

Question 3: Do small mammals respond to a particular spatial extent of landscapes, and does this extent change with study area, season or sampling scale?

Materials and methods

Study areas

The study was conducted in northeastern Alberta in three study areas between Owl River and Goodwin Lake, Alberta (about 55°N and 112°W) on a forest management area operated by Alberta-Pacific Forest Industries Ltd. (Figure 2-1). Sites were chosen to represent varying degrees of landscape heterogeneity caused by natural and anthropogenic disturbance that are presently common in this region. A reference study area (Figure 2-2a) was dominated equally by deciduous (trembling aspen, *Populus tremuloides*, and balsam poplar, *Populus balsamifera*) and conifer (primarily jack pine, *Pinus banksiana*, and black spruce, *Picea mariana*, with some mixed and white spruce, *Picea glauca*, patches), with small amounts of open water or marsh and young (less than 6 years) deciduous forests regenerating after harvesting. A second site (Figure 2-2b) had similar forest composition, but less conifer (a higher proportion of which was black spruce) and more harvested stands. This area (of which 11% of the landscape had been recently harvested) was called the managed area. The third site (Figure 2-2c), called the burned area, differed from the others in that the dominant landscape elements were burned black spruce and pine (1989 fire), with smaller patches of burned deciduous and undisturbed tracts of deciduous and conifer forests.

Permanent sampling grids were established at different spatial scales in each study area during 1996 (see Figure 2-2). Each area contained one "macro" grid with sampling points 1 kilometre apart, and two "meso" grids (labeled X and Y) with 250 metres between points. On the reference and managed areas, grids were installed systematically in a 7 x 9

(macro) or 8 x 8 (meso) arrangement, with points excluded when they fell in open bogs or where access was otherwise difficult. Meso grid locations were chosen to be representative of the landscape structure of their respective macro grid and to avoid large areas of wetland. All grids in the reference and managed areas contained a total of 64 sampling points each. The macro grid in the burned area contained fewer points (26) in an arrangement dictated chiefly by access, as did the Y-meso grid (9 points), with points only approximating 1000 and 250 m apart. The X-meso grid was set systematically, containing only 48 points due to the presence of a large bog in the northwest corner.

Study species

The species studied were *Clethrionomys gapperi* (red-backed voles) and *Peromyscus maniculatus* (deer mice). *C. gapperi* are microtine rodents and have been shown to be associated with shrubs and herbaceous ground cover, birch abundance, and coarse woody debris in aspen forests of this region (Roy *et al.* 1995). They are usually common in most forest types, particularly in mesic areas (Forsyth 1985, Burt and Grossenheider 1980, Whitaker 1980), though Green (1980) found that selectivity increased as density decreased from a peak phase. They feed on green vegetation, bark, seeds, nuts, roots, fungi and insects (Forsyth 1985, Burt and Grossenheider 1980, Whitaker 1980). Adults weigh 14 to 40 g and generally occupy home ranges around 0.1 ha (Burt and Grossenheider 1980).

P. maniculatus are cricitine rodents that are also common in most areas, but prefer dryer, more open habitats (Forsyth 1985, Burt and Grossenheider 1980, Whitaker 1980). Green (1980) found this species to be uncommon in willow, black spruce and jack pine habitats in this region. Local vegetation associations with birch, willow and grass cover, shrub species richness, small trees and large downed woody debris have been shown in aspen dominated forests (Roy *et al.* 1995). Food resources are primarily seeds, nuts and invertebrates (Forsyth 1985, Burt and Grossenheider 1980, Whitaker 1980). Adults weigh 18 to 35 g and home ranges are reported from 0.2 to 2.1 ha (Burt and Grossenheider 1980).

Additional species observed in incidental captures included woodland jumping mice *Zapus hudsonicus*, unidentified shrews, *Sorex* sp., meadow voles, *Microtus pennsylvanicus*, bog lemmings, *Synaptomys borealis*, and short-tailed weasels, *Mustela erminea*. These species all occurred in very low numbers and were not included in analyses.

Small mammal abundance

Live trapping at each grid sampling point was used to assess relative abundance of small mammals. Five Victor Tin Cat multiple-capture live traps were set at each point, one at the centre and one 35 m out in each cardinal direction (Figure 2-3). Traps were placed on grids and prebaited with oats and sunflower seeds for 2 to7 nights before trapping began. Trapping occurred over 2 to 4 nights at each point as detailed below. Traps were checked before noon each day and reset or removed. Traps were equipped with ample food and dry cotton bedding each time they were set. Upon capture, new individuals were sexed, weighed and marked with a yellow stripe on the white fur of their undersides using an aqueous picric acid solution. This mark generally stayed visible for at least 6 weeks such that previously caught individuals were not recounted in subsequent trapping nights. Abundance measures were simply the total number of different individuals of each species captured at a point.

Data from four live-trapping sessions were collected. The numbers of points and grids trapped varied among sessions due to weather, access and personnel limitations that changed over time. The first session (Sept. 1 to Oct. 10, 1996) was conducted on only the managed grids, with four consecutive trapnights at each point. The second (May 1 to June 16, 1997) was conducted on all nine grids for three consecutive nights at each point. The third (Aug. 24 to Oct. 6, 1997) was also conducted on all grids, but for only two consecutive trapnights per point. Similarly, the fourth session (May 1 to June 6, 1998) used a two-trapnight system, but only the managed and reference areas were trapped (minus the Y-meso grid on the reference site). In order to be sure that only over-wintered adults were included in spring abundance estimates, each spring data set was examined for first observation of adults in reproductive condition (perforate, pregnant or lactating females or scrotal males). Any animals caught after that time with low weights (generally less than 15 g), or that were noted as juveniles at the time of capture (based on size and pelage characteristics), were removed from the data set.

Landscape composition and configuration

Digital maps of forest cover were generated in geographic information systems (GIS) for each study area. The source data for these maps were Alberta Vegetation Inventory (AVI), provided by Alberta-Pacific Forest Industries Ltd. AVI is based on aerial photo

interpretation at a 1:20,000 scale and includes forest stand boundaries, composition and decade of origin based on canopy characteristics (Nesby 1997). To build landscape maps that were relevant to the species studied on these grids, landscapes were reclassified from the AVI into 11 forest types on the managed and reference grids, and 14 forest types on the burned grid. The main types included: agricultural open, harvested deciduous (regenerating *Populus* sp.), deciduous (*Populus tremuloides*, *P. balsamia*, *Betula paperifera*), jack pine (*Pinus banksiana*), black spruce/larch (*Picea mariana*, *Larix laricina*), white spruce (*Picea glauca*), mixed deciduous/pine, mixed deciduous/spruce, mixed pine/spruce, marsh (including open fens and bogs) and water. Additional burn types included: burned deciduous, burned pine and burned lowland.

To relate small mammal abundance to landscape structure, maps were "cookie-cut" from AVIs to create circular landscapes around each sampling point. Landscape extent (or size) was manipulated by generating maps within a number of radii around sample points. Landscapes were mapped within 50, 100, 250 and 500 m of sampling points. For each extent, FRAGSTATS software (McGarigal and Marks 1994) was used to quantify landscape structure. The output from this program included percent of the total area covered by each forest type in the landscape and a number of variables describing landscape configuration. Frequency distributions of percent cover for uncommon patch types were highly skewed, so a number of patch types were collapsed into five composition variables for statistical analyses. These variables included deciduous, conifer (primarily jack pine and pine/deciduous mixed forests), young harvested deciduous, young burned deciduous, and young conifer (burned pine and lowland black spruce). Each configuration variable used in this study represents some unique aspect of landscape configuration, is potentially ecologically important to the species and is standardized and thus comparable across landscape extents. Table 2-2 lists and describes each landscape variable used in analyses. Means and variances of each variable at each extent were compared among grids using frequency distributions, boxplots and descriptive statistics. This was done to determine any major differences among grids to facilitate later interpretation of landscape effects. Many variables exhibited different frequency distributions and variances that changed with landscape extent. For this reason, most variables were transformed (Table 2-2) prior to analyses.

Local vegetation

The structure and composition of local vegetation was assessed around each grid point during July and August 1996 and 1997. In order to characterize an area of roughly 3 ha around points, three 10 x 20-m plots were arranged systematically at each point and vegetation was analyzed in each plot. A centre plot positioned alternately 5 m east or west of the point was always used. Two other plots were laid out 65 m from the centre in two of three possible directions: north, southeast and southwest. The directions of outer plots were decided by systematically rotating through the possible combinations during the data collection in the field (Figure 2-4).

In each plot, many sampling techniques were used to evaluate vegetation characteristics. Cover scores were given for each shrub species present in the plot and for a number of ground cover classes including lichen, moss, grass, herbs, bare ground and leaf litter. Cover scores were coded 1-5, with 1 assigned to rare species of <1% cover or <5 stems, 2 assigned to species covering 1-10% of the plot, 3 for species with 10-20% cover, 4 for species with 20-50% cover, and 5 for those species covering >50% of a plot. Height of an average plant and cover was recorded in the shrub layer, which was usually less than 2 m tall, and the ground layer less than 20 cm tall. All trees (greater than 2 m in height) in each plot were counted and a size class was noted. Size class 1 was <8-cm diameter at breast height (dbh), 2 was 8.1 to 15 cm, 3 was 15.1 to 23 cm, 4 was 23.1 to 32 cm, and 5 was >32 cm. For alder and willow bushes, only stems greater than 4-cm dbh were counted because of the clumped distribution of these species. Fallen dead wood or coarse woody debris was quantified by counting all logs along the two 20-m sides of each plot that were greater than 8-cm diameter at their widest point. Each log was assigned to a size class as above. Similarly, all standing dead wood, or snags, within the plot that were greater than 8 cm in diameter and 50 cm tall were counted and assigned a size class.

Due to the high number of vegetation and coarse woody debris variables that could be generated from the vegetation sampling techniques, findings from previous work in the mixed-wood boreal forest (Roy *et al.* 1995) were used to select vegetation variables known to be associated with each species. Additional variables typical of conifer habitats (particularly jack pine) were also considered. Variables selected for *C. gapperi* included: total amount of coarse woody debris and large snags, number of aspen and birch trees, percent cover of shrub and ground-level vegetation, and cover scores for herbs, alder, and lichens. Variables

for *P. maculatus* included: amount of large coarse woody debris, number of small trees, number of aspen and birch trees, shrub species richness, and cover scores for grass, alder, willow, blueberry, and lichens. Table 2-3 shows the vegetation variables used for each species with a more detailed description of each. As with the landscape data, transformations were applied to some variables to standardize variance and normalize frequency distributions (Table 2-3).

Population spatial structure

Spatial structure in populations that was independent of other predictors was examined using geographic position of sampling points. Spatial data were collected in the field using Trimble Geoexplorer hand-held global positioning system (GPS) units. Satellite information used by these units to identify position was biased due to security procedures of satellite owners, so locations were corrected using base station data from Alberta-Pacific Forest Industries Ltd. Spatial data included Universal Transverse Mercator (UTM) coordinates, x (Eastings in metres) and y (Northings in metres) and seven other terms from a cubic trend surface regression of the form (after Legendre 1990, Borcard *et al.* 1992):

$$Z = ax + by + cxy + dx^2 + ey^2 + fx^2y + gxy^2 + hx^3 + iy^3$$

By considering these terms as predictors in regression, spatial structure or autocorrelation in east-west (x, x^2, x^3), north-south (y, y^2, y^3) and diagonal (xy, x^2y, xy^2) directions could be detected.

Statistical analysis

Each species was analyzed separately to look for associations with landscape composition and configuration, local vegetation and spatial position. Count data did not satisfy the assumption of a normal distribution of errors required for use of least-squares linear regression. This situation required the use of generalized linear models (GLMs) to model abundance (specifications: 'quasi-likelihood' family with a 'log' link function and 'mean' variance function; S-Plus Student Edition version 4.0, Mathsoft Inc.1998). Results from GLMs are given in terms of null and residual deviance. Deviance measures the amount of scatter around a linear model, incorporating the specified link and variance functions (Green and Silverman 1994). The null deviance is based on a model of "response = 1". Residual

deviance is the sum of deviance increments for each observation, and may be interpreted as the variation that is not be explained by the model. The amount of deviance that is explained by a model is calculated by subtracting the residual deviance from the null deviance.

The number of predictor variables available for these regressions was high, and multicolinearity was present. Therefore, GLMs were conducted using forward selection for variable entry. This procedure (using the "add1" command in S-Plus; Mathsoft Inc. 1998) involves fitting predictor variables one by one to a null (intercept only), or other model, and calculating Akaike's Information Criterion (AIC) for each potential model versus the original. The AIC is a penalized version of the log-likelihood function that can be used to evaluate the fit of a model (Akaike 1973, McCullagh and Nelder 1989). The variable that produces the lowest AIC statistic (provided it is lower than the original) is added to the model and the process is repeated, testing the remaining variables added to this new model. When no more variables can add significantly to the model (as tested by the AIC), the procedure ends.

Forward selection GLMs with explanatory variables from all predictor data sets were conducted for each small mammal data set (each grid in each trapping session at each landscape extent separately) to compute a full model giving the total deviance explained by all the predictors combined. In order to determine what part of that variation was due to pure effects of each predictor data set (landscape composition, landscape configuration, local vegetation, and spatial position) independent of the others, partial regression techniques were used as described by Legendre and Legendre (1998, pg. 532). The variables representing each predictor data set were removed in turn and the model was rerun each time with the remaining variables from the other predictor data sets. The difference between the residual deviance of the full and partial models gave the amount of deviance explained by the removed data set independent of the others. The sums of these pure components do not equal the total deviance explained by the full model, even though the same variables are used. This is due to interactions among predictor data sets that cause variables to explain more or less deviance in a full model (with other predictors) than in a model by themselves. Interactions represent the deviance that cannot be attributed to any individual predictor with confidence and so are of limited utility in this analysis and will not be discussed further.

Question 1: Quantifying and comparing predictors

Examinations of coefficients from GLMs were used to describe associations between abundance of each species and each predictor data set. To identify patterns of relative importance of each predictor data set, the deviance explained by the "pure" forms were entered into an Analysis of Variance (ANOVA) for each species at each landscape extent (SPSS version 9.0; SPSS Inc. 1999) with predictor data set being the main factor tested. Since the amount of deviance explained by each predictor was partially dependent on the full model from which it was derived, ANOVAs were blocked by response data set (*i.e* each grid in each trapping session; n=26 for 50 and 100-m extents and 9 for 250 and 500 m). Post-hoc comparisons were conducted when there was a significant effect of predictor ($p \leq 0.05$). The post-hoc methods used were Bonferonni paired T-tests between all possible pairs of predictors (Bonferonni corrected $\alpha = 0.05/6$ tests ≈ 0.001). The deviances explained in these analyses were not normally distributed. However, ANOVAs are robust to this assumption and, due to the exploratory nature of the analysis, this violation of assumptions was considered acceptable.

Question 2: Behaviour of predictors for different study areas, seasons and scales

Repeated measures ANOVAs were used as a tool to identify patterns in the deviance explained by each predictor within three main factors: study area, season, and sampling scale (SPSS Inc., 1998). Year was also entered as a main factor to account for annual variation, and season by scale (by year) interactions were included for tests of local vegetation and spatial position and study area by season interactions for tests of landscape composition and configuration. Landscape extent was the "within-subjects" factor. All response data sets (n=26) were used for testing for effects at the 50 and 100-m landscape extents. Only the nine macro grid samples were used for testing for effects at the 250 and 500-m extents because regressions were not conducted at these extents on meso grids due to non-independence of landscapes greater than a 125-m radius. Differences among levels of significant or marginally significant ($p \cong 0.100$) main factors and interactions were interpreted by examining group means or by Bonferonni T-tests (giving adjusted p-values).

Question 3: Comparing landscape extents

The repeated measures ANOVAs described above also served as a means of comparing landscape extents since any significant within-subjects factor or interaction suggested that extents differed. Examination of means within each extent was used to interpret the nature of differences. The data for all ANOVAs failed to satisfy the repeated measures assumption of sphericity, so an adjusted F-statistic was used for testing within-subjects factors called the Greenhouse-Geisser. This adjustment is more conservative than some other adjustments, minimizing the chances of committing a type I error (von Ende 1993).

Results

Small mammal abundance

Over the entire duration of the study (approximately 16,080 trapnights), the number of individuals captured totaled 4,673 for *C. gapperi* and 3,056 for *P. maniculatus*. Figure 2-5 summarizes abundance per point per trapnight in each study area, after the first 2 days of trapping in each session. Seasonal fluctuations were higher for *C. gapperi* and numbers seemed be to be increasing from 1997 to 1998, with many more individuals captured in spring 1998 than in spring 1997. This pattern suggests that *C. gapperi* populations were likely in an increasing phase, but had not yet achieved peak densities. *Peromyscus maniculatus* was most abundant on managed grids, while *C. gapperi* was found in similar abundance in all areas.

Landscape composition and configuration

Means and variances for each landscape variable at each landscape extent on each study grid are presented in Appendix 1. Other data presented on ranges of values come from examinations of box plots and frequency distributions for each variable.

There were differences in means and frequency distributions of variables across landscape extents. However, unless otherwise noted, the differences among extents were the same for all grids. There were differences in landscape composition among study grids. Deciduous forest was more abundant on managed grids, particularly the X-meso grid, while this habitat was less common on all burned grids and on reference meso grids. The range in

the amount of deciduous was high among points on all grids, with the exception of the burned Y-meso where most points contained no deciduous forest (at the 50 and 100-m extents). The amount of conifer was low on burned grids and managed meso grids, intermediate to high on the managed and reference macro grids, and highest on reference meso grids. Young forest resulting from harvesting was rare on the managed X-meso and all reference grids (though variability on the managed X-meso was high) and absent from burned grids. Similarly, young forests created by burning were absent from the reference and managed grids. Deciduous burns were abundant on the burned Y-meso grid, and conifer burns were fairly rare around points on all burned grids.

Landscape configuration was less variable across grids than composition, though some differences were present. Edge density was higher on the managed macro grid than on the other macro grids, though this was only evident at smaller landscape extents. It was also relatively high on the reference and burned X-meso grids, for all landscape extents. The largest patch index on the burned macro grid was less variable at all extents than on other grids. Mean shape index and patch density were consistent across grids for all extents. However, patch richness density had a wide range of values on the managed macro grid at all extents, but was usually high on the burned X-meso grid points at the 50-m radius extent. Simpson's Evenness Index was high on the burned meso grids at all landscape extents.

In general, landscape structure was fairly similar across areas except for changing composition due to the amount of disturbance or conifer patch types, and greater amount of heterogeneity in the burned area than the others. In addition, all variables changed similarly across extents among study areas and all were correlated across extents within a study area.

Question 1: Quantifying and comparing predictors

A total of 70 forward selection GLMs were run for each species. This included a model for each small mammal data set (by grid and trapping session) at each landscape extent (all four radii for macros and 50 and 100-m radii for meso grids). The boxplots in Figure 2-6 show the average and distribution of the deviances explained by the full models for each species at the different landscape extents. The deviance explained ranged from 2 to 187, with values varying similarly among models across extents. Full models appear to explain similar amounts of deviance for both *C. gapperi* and *P. maniculatus* at all extents, but further examination from partial regressions shows relative differences in response by each species

to the four predictor data sets of interest (landscape composition and configuration, local vegetation and spatial structure).

Landscape composition entered 48 of the models (69%) for *C. gapperi*. The most common relationships included a positive association with young deciduous from harvesting and a negative association with conifer. Landscape configuration variables contributed to models in 32 cases (46%). No particular variable was more common than any other was, so models were characterized as representative of positive or negative associations with landscape heterogeneity. Landscape heterogeneity was defined by increasing edge density, patch density, patch richness density, and Simpson's Evenness Index, and by decreasing largest patch index and mean shape index. Relationships to landscape heterogeneity are quantified in Table 2-4 for each study area. There are generally no patterns in *C. gapperi* response to landscape heterogeneity, except for predominately positive associations in the reference study area. Sixty-five (93%) of the full models generated for *C. gapperi* included one or more local vegetation predictors. The most common and consistent relationships (with respect to sign) included positive associations with large snags, coarse woody debris, herb cover and birch trees, and negative associations with alder shrubs. Forty of the models (57%) incorporated spatial position indicating spatial autocorrelation. No spatial variable dominated these relationships and the direction of spatial structure differed among grids and among seasons on the same grids.

The average amounts of deviance in *C. gapperi* abundance explained by each of the four predictor data sets is shown in Figure 2-7a. ANOVAs indicated a significant difference in deviance explained among predictors at the 100-m landscape extent ($F = 6.063$, $p = 0.001$). Post-hoc T-tests showed that this difference was manifested in a significantly greater amount of deviance explained by local vegetation than by landscape configuration ($p < 0.001$). At all extents, there was a trend for local vegetation to explain the most deviance on average, followed by landscape composition, spatial position, and finally landscape configuration.

For *P. maniculatus*, landscape composition entered 43 of the 70 regression models (61%). The most common relationships included positive associations with mature ands young deciduous forests and negative associations with conifer. Landscape configuration variables contributed to models in 23 cases (33%). As with *C. gapperi*, no variable was particularly common, so models were characterized by their association with landscape

heterogeneity (Table 2-4). *Peromyscus maniculatus* relationships with heterogeneity were also inconsistent, with the exception of predominately negative associations on the burned study area. Sixty-four of models for *P. maniculatus* (91%) included one or more local vegetation predictors. The most common and consistent relationships included positive associations with alder and negative associations with small trees, birch trees, lichen, blueberry and willow shrubs. Only 21 of the models (30%) incorporated spatial position. Spatial structure differed among grids and among seasons on the same grids, but most trends were in an east-west direction.

The average amounts of the deviance in *P. maniculatus* abundance explained by each predictor data set is shown in Figure 2-7b. ANOVAs indicated a significant difference among predictors at all landscape extents ($F \geq 5.479$, $p \leq 0.005$). Post-hoc T-tests with conservative Bonferonni adjustments of probabilities showed that at the 50 and 100 m extents, local vegetation explained significantly more deviance than landscape configuration ($|t| \geq 3.907$, $p \leq 0.001$). At the 100-m extent, there were also significant differences between the deviance explained by configuration and composition and by vegetation and spatial autocorrelation ($|t| \geq 3.804$, $p \leq 0.001$). The general trend at all extents was that the greatest amount of deviance was explained by local vegetation, followed by landscape composition, spatial structure and landseape configuration.

The order of importance of predictors was the same for both species, but local vegetation was a better predictor of abundance for *P. maniculatus* than for *C. gapperi*. There remains a large amount of variation in the deviance explained by each predictor that may be explained by difference in study areas, seasons, and spatial scales of measurement. This will be explored further in the following section.

Question 2: Behaviour of predictors for different study areas, seasons and scales

The deviance explained by landscape composition for *C. gapperi* in all grid samples showed marginally significant differences among study areas ($F = 2.630$, $p = 0.101$) and seasons ($F = 3.881$, $p = 0.065$), but did not differ between scales or among years, and there was no interaction between study area and season. Landscape composition explained the most deviance in the managed study area and during the fall trapping season (Figure 2-8a). For the deviance explained by landscape configuration, there were significant effects of study

area ($F = 6.956$, $p = 0.006$) and a study area by season interaction ($F = 4.762$, $p = 0.023$) when all grids were included in the ANOVA (Figure 2-8b). Post-hoc T-tests showed that the deviance explained by configuration was greater on reference sites than on managed sites (Bonferonni-adjusted $p = 0.034$), with greater seasonal differences there as well. These trends with landscape structure were less robust when testing only among the nine macro grid samples, though the study area by season interaction was still marginally significant ($F = 157.094$, $p = 0.056$) for landscape configuration effects.

When considering local vegetation effects on *C. gapperi*, there were no differences among study areas, seasons or sampling scales when analyzed for macros alone. However, when all grids were considered, there was a season by scale interaction ($F = 6.048$, $p = 0.026$) and a weak season by scale by year interaction ($F = 2.660$, $p = 0.101$) (Figure 2-8c). This was caused by a greater amount of deviance explained by local vegetation on managed meso grids than on the macro grid in fall 1996. The amount of deviance explained by spatial structure changed in a similar manner (Figure 2-8d). Season showed significant effects when examined either across all grids or on macros alone ($F \geq 4.980$, $p \leq 0.038$). Study area showed marginally significant effects when all grids were included ($F = 2.691$, $p = 0.094$) as well as season by scale ($F = 5.418$, $p = 0.033$) and season by scale by year ($F = 5.411$, $p = 0.016$) interactions. These differences are probably caused by a high amount of deviance explained on the managed macro grid in fall, 1996 compared to the low amounts explained on the mesos in that session.

When all grids were analyzed, the amount of deviance in *P. maniculatus* abundance explained by landscape composition showed evidence of seasonal differences ($F = 2.615$, $p = 0.124$). These may be explained by a weak study area by season interaction ($F = 2.401$, $p = 0.121$) where stronger effects occurred in fall only on reference sites (Figure 2-9a). When considering only macro grids at all landscape extents, study area and season both had marginal effects on the deviance explained by landscape composition ($F = 89.532$, $p = 0.075$ and $F = 33.777$, $p = 0.108$, respectively). There were no trends in deviance explained by landscape configuration with respect to study area, season or sampling scale when analyzed for all grids or for macros alone.

When considering local vegetation effects on *P. maniculatus* on all grids, there were weak effects of season and sampling scale ($F = 2.902$, 0.105 and $F = 2.776$, $p = 0.112$) due to a larger amount of deviance explained by vegetation in fall than in spring and on macro

grids than on mesos. A marginally significant season by scale interaction ($F = 3.912$, $p = 0.065$) indicated that individual season and scale effects were due to greater deviance explained by local vegetation in fall on macro grids only (Figure 2-9b). No differences were found when considering macro grids alone. Spatial structure in *P. maniculatus* did not change with study area, season or sampling scale when considering macros alone, but did show a season by scale interaction when all grids were analyzed ($F = 4.877$, $p = 0.042$). This resulted from greater deviance explained by spatial position on meso grids than on macro grids in the fall season.

In summary, the effects of landscape composition are greatest in fall for both species, but this is only evident on the reference study area for *P. maniculatus* whereas composition is always more important on the managed study area for *C. gapperi*. Configuration effects increase from spring to fall on the reference study area for *C. gapperi*, but there are no changes in *P. maniculatus* response. Local vegetation predicts *C. gapperi* abundance best in the fall on meso grids, while *P. maniculatus* abundance is best predicted by local vegetation on macro grids, also in the fall. Spatial structure is most evident on the managed macro grid in fall, 1996, for *C. gapperi* and is highest on meso grids in fall for *P. maniculatus*.

Question 3: Comparing landscape extents

When all landscape extents were compared using data from macro grids, no predictor showed differences among extents for *C. gapperi*. However, when all response data sets (macro and meso grid samples) were included for 50 and 100-m extents, landscape extent caused differences in the ability to detect spatial structure ($F = 12.741$, $p = 0.003$), and there were also extent by scale ($F = 11.915$, $p = 0.003$), extent by year ($F = 5.982$, $p = 0.011$), extent by season by scale ($F = 9.355$, $p = 0.008$), and extent by season by scale by year ($F = 3.583$, $p = 0.052$) interactions. Spatial structure predicted abundance better when analysis was conducted at a 100-m extent than at a 50-m extent, but only on the managed macro grid during 1996, accounting for the interactions observed above. Other predictor data sets continued to show no differences among extents when all response data sets were included in the analysis.

Repeated measures ANOVAs for deviance in *P. maniculatus* abundance explained by landscape composition, configuration and spatial position showed no differences among

extents when analyzing all extents in macro grid samples. However, there were significant differences in the deviance explained by local vegetation among extents ($F = 24.433$, $p = 0.004$), an extent by year interaction ($F = 10.590$, $p = 0.016$) and weak extent by study area ($F = 4.143$, $p = 0.088$) and extent by season interactions ($F = 3.488$, $p = 0.123$). Differences among extents were most pronounced in 1996 on the managed macro grid, where local vegetation explained much more deviance at 500 m than at other extents. When all response data sets were used for testing *P. maniculatus* response between 50 and 100-m extents, there was no effect of extent on the deviance explained by landscape composition. However, the deviance explained by landscape configuration showed a marginally significant change with extent ($F = 2.990$, $p = 0.102$), with greater effects at 100-m than at 50-m extents. The absolute value of the difference was very small (< 3.8), so this difference is negligible. As in the macro grid analysis, the amount of deviance explained by local vegetation was affected by landscape extent ($F = 21.185$, $p < 0.001$), and there were interactions between extent and sampling scale ($F = 11.184$, p 0.004) and extent and year ($F = 4.382$, $p = 0.030$). These interactions resulted from higher deviance explained by local vegetation at 50 than 100-m extents on the managed macro grid in 1996. Similarly, the ability to detect spatial structure changed with extent based on year ($F = 3.070$, $p = 0.074$) and there was a weak extent by season by scale by year interaction ($F = 2.635$, $p = 0.103$). This was caused by a greater difference between macro and meso grids (spatial structure being higher on meso grids) at 100 m than at 50 m on the managed study area in fall 1996.

In general, there was no landscape extent where landscape effects were significantly greater for either species. Effects of local vegetation did not change with landscape extent for *C. gapperi*, but did differ with extent for *P. maniculatus* on managed grids in fall 1996. Landscape extent altered the ability to detect spatial structure in populations of both species in fall 1996 (though it was only evident for *P. maniculatus* when meso grids were included in analysis).

Discussion

Landscape structure has been shown to affect animal populations in many regions of the world. However, other studies have not partitioned these effects from those of local vegetation or coincident spatial patterns. By statistically controlling for covariates, this study

isolates effects of a number of predictors and provides insight into the true magnitude of landscape effects under a variety of circumstances.

Question 1: Quantifying and comparing predictors

As expected, landscape structure in the boreal forest did affect small mammal populations. However, local vegetation explains the most variation in abundance for both *C. gapperi* and *P. maniculatus*. This is likely because small herbivores with high metabolisms and many predators require specific resources and shelter that are provided by local vegetation. However, the difference between the explanatory contributions of landscape structure and local vegetation was smaller for *C. gapperi* than for *P. maniculatus*. Ruefenacht and Knight (1995), in a study of the use of corridors of different gap sizes and width by *P. maniculatus*, found that the most important variable determining corridor use was tree density and that corridor characteristics only affected use under specific local habitat conditions. For *P. maniculatus*, effects of landscape structure appear to be mediated by, or are minor relative to local vegetation effects. The lower amount of deviance explained by local vegetation for *C. gapperi* might indicate that habitat selection by this species occurs at larger scales, perhaps due to more general habitat requirements. Higher abundances of *C. gapperi* compared to *P. maniculatus* on the reference and burned study areas, where sampling points are more evenly distributed among forest types, also suggest that *C. gapperi* may be a more generalist species in this region.

Spatial structure was not the least important source of variation as predicted, but it still explained very little deviance in abundance for either species. Changes in the spatial variables entered at different landscape extents, within the same small mammal data set, were the result of these being relatively weak predictors among others in the regression models. However, the fact that spatial variables entered the models at all indicates that either abundance was related to some spatially structured environmental variable that was not measured, or that there was some directional population process (*i.e.* dispersal) causing spatial structure in the populations (Legendre and Fortin 1989, Borcard *et al.* 1992, Rossi and Quénéhervé 1998). Most environmental variables thought to be relevant to small mammals were submitted to regression analyses, with the exception of local predator and competitor abundance. It is unlikely that the observed spatial structure was caused by some stationary (*i.e.* vegetation or microclimate) variable, since the direction of spatial trends changed with

different trapping periods. Bowman and Forbes (personal communication) have also noted spatial autocorrelation in these species across large study areas in New Brunswick, Canada, with no apparent link to spatially structured vegetation variables. Therefore, it is probable that the population spatial structure resulted from dispersal events or community-level interactions, neither of which was quantified directly in this study.

The amount of habitat in the landscape was the most important aspect of landscape structure for predicting small mammal abundance. *C. gapperi* increased with the amount of harvested land, which local vegetation associations with coarse woody debris and herb cover suggest are a good habitat type. *C. gapperi*'s positive associations with large snags, coarse woody debris, herbs and birch also suggest that this species may have an affinity for older or regenerating deciduous stands. Roy *et al.* (1995) also found that *C. gapperi* was associated with mature aspen in this region. However, the availability of mature or recently burned deciduous stands at a landscape scale did not generally affect populations in this study. The relationship may not have been detected in this analysis due to the lack of detail in maps in terms of forest age, and to the absence of burned deciduous forest at most sample points. There was a negative association between *C. gapperi* abundance and the amount of conifer in the landscape, and jack pine localities generally had fewer individuals than deciduous ones. A negative association with alder (a common shrub in jack pine stands) weakly supports the idea that this species avoids conifer stands, but characters more representative of pine forest failed to enter models.

The positive association with deciduous and harvested forest in the landscape for *P. maniculatus* was not supported by local vegetation results. But it did explain why abundance of this species was highest on the managed grid, where the amount of these forest types is high relative to other areas. *P. maniculatus* responded positively to alder abundance, though not due to an affinity for jack pine, since few animals were ever captured in pine forests and there were negative associations with small trees, blueberry and lichen, which are all characteristic of pine communities. These negative associations help explain this species' negative relationship with conifer forest at a landscape scale.

C. gapperi abundance increased with habitat heterogeneity most commonly on reference study areas, confirming the prediction that heterogeneity is important in landscapes with large amounts of poor quality habitat. These grids contained higher than average amounts of jack pine, which has been shown to be negatively associated with *C.*

gapperi abundance. Heterogeneity, or patchiness, in these landscapes may increase connectivity among good habitat patches, or cause more poor quality habitat to be occupied because of increased encounter rates during dispersal.

P. maniculatus populations did not show consistent positive associations with landscape heterogeneity on the reference grids like *C. gapperi* did. Heterogeneity would only be beneficial if some intermediate, or matrix, forest type inhibited movement between two habitat patches. Landscape effects on populations decrease when the species concerned exhibits very long-distance (relative to the scale of landscapes considered) and non-directional dispersal (Fahrig and Paloheimo 1988b). *P. maniculatus* may satisfy these conditions, or it may have movement capabilities that are unaffected by the quality of the habitat being traversed. Anecdotal evidence and homing experiments suggest that *P. maniculatus* may travel upwards of 1800 m through forested habitats (Teferi and Millar 1993b, Bowman and Forbes 1999), which exceeds the scales of landscapes used in this study. However, this information is based on rare movement events and homing experiments with artificially transplanted individuals, and is probably not indicative of the normal dispersal behaviour of this species.

Another explanation for the lack of a strong positive response of *P. maniculatus* to landscape heterogeneity could be a smaller pool of dispersers in this population relative to *C. gapperi*. It is common for microtine rodents such as *C. gapperi* to show greater increase in numbers over a breeding season than cricitines like *P. maniculatus* (Banfield 1974). Gilbert and Krebs (1991) noted that red-backed vole populations (*C. rutilis*) had greater seasonal fluctuations than *P. maniculatus* in southwestern Yukon, and attributed this to the voles' faster sexual development (breeding occurred in the first year) and longer breeding season. Similarly, in a study in northeastern Alberta, Weaver (1996) found higher recruitment and juvenile growth rates in *C. gapperi* than in *P. maniculatus*. Higher reproductive output by *C. gapperi* is indicated by greater seasonal fluctuations in the present study, and may have resulted in a larger number of dispersers in these populations, causing a greater response to landscape heterogeneity in fall.

Population spatial structure also provides insight into the size of the pool of dispersers in each species. Spatial position was, on average, a better predictor of abundance for *C. gapperi* than for *P. maniculatus*, indicating that they have more distinct spatial structure. This structure may be caused by dispersal from areas of high density, indicating a greater

number of *C. gapperi* moving through these landscapes to produce large-scale spatial patterns. *C. gapperi* have been shown to reach sexually maturity in their year of birth in the Yukon to the north (Gilbert and Krebs 1991) and Kananaskis to the south (Innes and Millar 1990, Innes and Millar 1993, Teferi and Millar 1993a), whereas *P. maniculatus* typically do not. A similar pattern has been observed near my study area, with only slightly higher tendencies for *P. maniculatus* to mature in their first year (about 12%) (R. Moses, unpublished data). If summer dispersal is triggered by a need to establish home ranges upon sexual maturation, then *C. gapperi* populations can be expected to have more dispersers during the summer and fall, even if overwintered animals of both species produce the same number of offspring during that time. A difference in disperser numbers like this could explain the weaker relationships of *P. maniculatus* to both landscape structure and spatial position relative to *C. gapperi*.

Landscape heterogeneity has thus far been discussed in terms of its benefits to animal populations by providing connectivity in landscapes dominated by poor habitat. However, it can be argued that increased heterogeneity involves smaller patches of good habitat, which may result in higher probabilities of local extinction (MacArthur and Wilson 1967). The only situation in this study where heterogeneity resulted in consistently negative associations with abundance was with *P. maniculatus* on the burned grids (though the deviance explained was low). The lack of strong associations of *P. maniculatus* with burned forest types in composition and vegetation analyses suggests that there was no strong avoidance of these habitats and movement through them was not difficult. If dispersal were unlimited or local populations were maintained without any dispersal at all, there would be no advantage of landscape heterogeneity, even when densities were low. The best situation in either case would be to have good quality habitat in larger patches, so that breeding populations could be maintained at some minimum level. Area on the burned grids was more evenly distributed among patch types than on other grids (high Simpson's Evenness Indices), and patch richness density was high at small radii on the burned x-meso. These trends suggest that forest patches on the burned study area may be smaller and more isolated than in the other study areas. The very low number of *P. maniculatus* on burned grids probably resulted from the fact that good quality habitat (deciduous) was more difficult for dispersers to find on the landscape. The negative effects of habitat isolation would have been augmented if the matrix habitats were temporarily usable and functioned as dispersal

sinks, discouraging long-distance movements to other patches of good, or source, habitat (Pulliam and Danielson 1991). No previous studies have identified minimum size or maximum isolation of habitat patches for *P. maniculatus*, but the lower reproductive capacity of this species probably makes it more prone to adverse effects of patch size and isolation than *C. gapperi* is. Comparing results across grids supports this idea, since *P. maniculatus* abundance was similar on both reference and burned study areas, but deciduous habitat was not restricted to small isolated patches on the reference, so heterogeneity did not reflect patch size limitations.

Question 2: Behaviour of predictors for different study areas, seasons and scales

Comparing effects of each predictor in different study area, seasons and sampling scales provided further insight into the biology of the study species in this region. The most consistently significant factor affecting the deviance explained by all predictors was season, with higher deviance in fall than in spring. These results may be criticized because fall data sets contained a greater number of animals, producing response data sets that were less skewed than in spring and so may have been more appropriate for regression analyses. However, the quasi-likelihood family of GLMs used for these analyses performs iterations on response data to estimate a dispersion parameter that is specific to the data set being analyzed. It is possible that spring abundance was sometimes so low that parameter estimation was less accurate than in fall models, but for the remainder of this discussion, it is assumed that differences in data dispersion are accounted for by the quasi-likelihood method.

The magnitude of local vegetation effects was fairly constant for *C. gapperi* abundance, with the exception of higher amounts of deviance explained by vegetation on managed meso grids in 1996 than on the macro grid in that same year. The vegetation variables contributing to these models were the number of aspen trees and the amount ground cover, both of which were very high in harvested stands. The meso grids contained a greater number of sampling points in harvested stands than the macro (Figure 2-2c) and it was observed that these areas supported an especially high number of *C. gapperi* at that time. Spatial position was a good predictor of abundance for this species during fall 1996 on macro grids. These two results together suggest that harvested stands on meso grids

functioned as source habitat and that dispersers may have radiated from these local hot spots to create a spatial pattern of abundance at a very large scale.

P. maniculatus also showed a season by scale interaction for vegetation effects on abundance. Vegetation was a better predictor on macro grids than on mesos in the fall. Scale differences were likely driven by greater variation in willow and blueberry cover (important predictors of *P. maniculatus* abundance) over these larger areas, producing better regression models. The seasonal difference likely indicates a strong vegetation effect on recruitment since more deviance is explained in fall. This species has also been shown to increase feeding and cache food in late summer and fall in preparation for winter (Seabloom *et al.* 1994), so the quality of local resources is more important in fall and individuals may be more selective in their choice of habitats at this time. This is contrary to the prediction that spring abundance would reflective of local habitat quality and so produce the best models with local vegetation. Other studies in northern populations suggest that age is the only good predictor of overwinter survival, rather than home range characteristics (Millar and Teferi 1993).

Results from analyses of population spatial structure in the fall (which is likely caused by dispersal) provide insight into connectivity of landscapes in each study area, and illustrate why landscape heterogeneity may be important for *C. gapperi* on reference sites. Connectivity was likely highest for both species on managed grids, due to the large amounts of deciduous and harvested habitat and low amounts of conifer. In support of this assumption, *C. gapperi* populations exhibited the greatest spatial structure on these grids. Dispersal seemed to be moderate for this species in the burned study area (as indicated by intermediate levels of deviance explained by spatial position on these grids). This was expected since no habitat in that area was identified as particularly good or bad in local vegetation or landscape composition analyses. There was no effect of study area on spatial structure in *P. maniculatus* populations, which supports earlier speculations that connectivity was unimportant to distribution and abundance of this species.

Scalar differences in spatial structure give some indication of average distances moved by the two species. Spatial structure in fall was higher on macro grids for *C. gapperi*, and on meso grids for *P. maniculatus*, suggesting that dispersal may occur over larger distances in *C. gapperi*, producing patterns over kilometres-wide areas. Steen *et al.* (1996) reported population synchrony at scales of up to 40 km in *Clethrionomys glareolus* in Norway

and attributed this partly to dispersal processes causing autocorrelation over large spatial scales. Detection of spatial structure would also be limited to macro grids if the average size of high-density patches meets or exceeds the size of a meso grid. Patches of this size could only be revealed at a macro scale. If dispersers radiate from local source habitats, as was suggested for harvested areas earlier, an increase in the number of dispersers would require that a greater proportion move longer distances, creating larger patches of high density. Spatial structure in *P. maniculatus* was greatest on meso grids in fall, indicating that the scale of patchiness for this species' population is smaller than a meso grid. If there were local source habitats, high-density patches would likely not spread as far for *P. maniculatus* as for *C. gapperi* if the assumption of fewer dispersers were correct. King (1983), in an experimental setting in Michigan, found that juvenile *P. maniculatus* remained close to their place of birth even after maturation and dispersal. *Peromyscus leucopus* in Indiana showed dispersal distances at relatively small scales as well, with individuals being highly philopatric and rarely dispersing farther than 250 m from the natal home range (Kearne 1990). Delayed maturation of *P. maniculatus* in Alberta likely results in shorter dispersal distances as well, because waiting until the following year to breed could allow individuals to occupy areas closer to their natal home ranges since neighbouring adults (> one year old) have lower overwinter survival (Millar and Teferi 1993).

An alternative cause for the large-scale spatial patterns seen in *C. gapperi* is predation. Short-tailed weasels (*Mustela erminea*) are major predators on small mammals in this ecosystem and occupy home ranges up to 16 ha (Burt and Grossenheider 1980). It has been shown, on study sites overlapping those used in this study, that weasels consume primarily *C. gapperi*, not *P. maniculatus* (Lisgo, 1999). Spatial patterns of weasels may therefore be responsible for spatial structure of *C. gapperi* populations at the macro grid scale, rather than longer dispersal. The fact that population spatial structure changes with season could counter the argument for predation though, since this process should be constant temporally and spatial structure was only strongly evident in the fall.

There was no effect of sampling scale on the deviance explained by landscape structure, indicating that meso grids provided an adequate sample of landscapes that was not improved by sampling over larger, more costly spatial extents. However, there is evidence that landscape effects are dependent on study area and season. *C. gapperi* abundance was predicted best by landscape composition on the managed study area. The positive

association of this species with harvested deciduous forest likely caused this study area effect, since harvested forest was only common on managed grids. In addition to study area effects, composition had greater effects on abundance in fall than in spring. *C. gapperi* was also affected significantly more in fall by landscape configuration, but this difference was restricted to the reference study area. Similarly, *P. maniculatus* was predicted best by landscape composition in the fall on reference grids.

The greater effects of landscape structure in the fall season are assumed to reflect influences on local recruitment through immigration, since dispersal occurs primarily during late summer and fall and likely contributes to fall distributions. The improvement of composition models with *C. gapperi* abundance in fall suggests that the amount of source habitat may affect abundance throughout the landscape. Jack pine was very abundant on the reference grids, and this habitat has been shown previously to be sub-optimal for both species. The increased effect of configuration on *C. gapperi* abundance in fall on reference grids supports the prediction that the presence of dispersal barriers in the form of sub-optimal habitat augments the effect of landscape structure on populations. *P. maniculatus*, as with *C. gapperi*, requires more suitable habitat in the landscape for increased local recruitment. However, seasonal differences in composition effects are present only on the reference study area for this species. This may be because of a wider range in the amount of good habitat (including both deciduous and harvested forest) on the reference study area. On the managed grids, there tends to always be a large amount of good habitat in the landscapes, whereas there is always very little in landscapes on the burned study area. These limited ranges in variability of amount of suitable habitat for *P. maniculatus* may have resulted in less deviance explained by composition in these study areas. The absence of increased effects of landscape configuration during the fall on *P. maniculatus* provides evidence that dispersal is not affected by landscape connectivity for this species.

Question 3: Comparing landscape extents

The absence of a radius effect on the deviance explained by local vegetation for *C. gapperi* was expected since the same vegetation variables were submitted to the model at all extents. However, the deviance explained by spatial position was higher at 100 m extents than at 50 m for *C. gapperi*, which was evident mainly on the macro grid in fall, 1996. The regression model for the 50 m radius extent of this data set contained a configuration variable (Simpson's Evenness Index) that did not enter at 100 m. When evenness was no longer a good predictor at 100 m, spatial position explained more deviance, probably because of spatial pattern of 50-m landscape evenness. This difference seems to be driven by one data set and, since spatial structure in this case reflects response to configuration, it reveals nothing informative about population processes like dispersal.

The radius effects on deviance explained by local vegetation and spatial position in *P. maniculatus* occur for the same reason as the *C. gapperi* example above. These instances of forward selection causing differences between models demonstrate how intercorrelations can sometimes result in different outcomes depending on the explanatory variables submitted. As landscape variables change slightly among extents, their relationship with the response improves or weakens. When spatial or vegetation variables were correlated with landscape variables, only the best predictor enters each model, and the relative importance of covariates sometimes changes as landscape variables change with extent. However, there were no differences among landscape extents for the deviance explained by landscape structure for either species studied. Larger landscapes were expected to produce better models if dispersal was driving the species' response, whereas small landscapes would be best for small-scale effects on foraging or home range selection. The failure to detect a 'best extent' may indicate that the same process (likely dispersal) produced effects at all extents studied. This is supported for *C. gapperi* in this region, where home range or activity radii have been documented at around 20 to 25 m for females and 40 m for males (Bondrup-Nielsen 1987, Weaver 1996). Data on average home range size for *P. maniculatus* are not available for this region, but are likely similar based on body size.

Failure to detect radius effects may have also resulted from the strong correlation of landscape variables across extents and high amounts of variance relative to means for response to landscape structure. These limitations in the data limit the ability to detect differences using conventional statistics.

Conclusions

It is evident that landscape structure has an influence on spatial patterns of abundance of *C. gapperi*, and to a lesser extent, of *P. maniculatus* when measured during the fall. The difference between these species may result from a larger pool of dispersers in *C. gapperi* populations, and perhaps longer average dispersal distances of this species relative to *P. maniculatus*. *C. gapperi* responded more to landscape composition in fall in all study areas suggesting its importance to recruitment by dispersal, and composition had the greatest effects on this species on the managed study areas where harvested forest (a good habitat type) was common. In this study however, the area where landscape seems to be the most important is the reference study area, where poor-quality jack pine forest is very abundant and configuration results suggest it may cause barriers to dispersal for *C. gapperi*. When landscape was important for *P. maniculatus*, it was generally restricted to compositional effects in fall, with no consistent relationships to landscape configuration except on sites where heterogeneity caused optimal habitat to be rare and discontinuous (*i.e.* the burned landscape). These observations demonstrate the need for ecologists to consider the effects of landscape structure on species individually. Knowledge of a species' dispersal behaviour in different forest types and the proportion of the population that disperses may allow for prediction of how that species will respond to structure.

Although landscape structure may improve models of abundance, local vegetation remains the best tool for predicting small mammal abundance and aids in interpreting landscape effects. Spatial autocorrelation is also an important consideration during or after periods of dispersal and can reveal clues about landscape connectivity and dispersal ranges without conducting in-depth studies on movement. The concentric-circle approach to isolating the extent where small mammals respond best to landscape structure seems to be inadequate in this region. This may be due to high variability in landscape response and the self-similar, or fractal, nature of these landscapes at the spatial scales considered. However, it is probable that the stand-level landscapes measured in this study were all within the spatial scale of dispersal of the two species, causing no change in magnitude of effects with scale. Reducing the grain of sampling for both small mammals and landscape in future work may allow detection of composition and configuration effects at a foraging scale.

The mixed-wood boreal forest of northeastern Alberta may be added to the growing list of ecotypes where landscape structure has been shown to affect animal populations. But even among separate study areas in the region, there is little generality of effects. This is due to a number of factors, most notably study species, landscape context (relative amounts of good and poor habitats) and season. Further research should now focus on testing the mechanisms of these differences.

Table 2-1. Hypotheses and predictions concerning each research question.

Question	Hypotheses and predictions
1	1. There are differences in the explanatory contributions of landscape structure, local vegetation and spatial autocorrelation. *Prediction:* Local vegetation explains the most variation in small mammal abundance, followed by landscape structure, then spatial autocorrelation.
2	3. Effects of landscape structure vary with season. *Prediction:* Landscape effects are greater in fall than in spring. 4. Effects of landscape structure vary with study area. *Prediction*: Landscape structure affects abundance the most on landscapes where dispersal barriers are present or good habitat is rare, such as the reference or burned study areas. 5. Effects of landscape structure vary with sampling scale. *Prediction:* Landscape structure is a better predictor on macro grids than on meso grids. 6. Effects of local vegetation vary with season. *Prediction*: Vegetation effects are greater in spring than in fall. 7. Effects of local vegetation do not vary with landscape type. 8. Effects of local vegetation do not vary with sampling scale. 9. Spatial autocorrelation varies with season. *Prediction*: Autocorrelation is greater in fall than in spring. 10. Spatial autocorrelation varies with study area. *Prediction*: Autocorrelation is greatest on landscapes with high connectivity (*i.e.* with lots of continuous high-quality habitat). 11. Spatial autocorrelation varies with sampling scale. *Prediction*: Autocorrelation is greater on meso grids than on macros.
3	12. Effects of local vegetation and spatial autocorrelation do not change with landscape extent. 13. Effects of landscape structure vary with landscape extent. *Prediction*: Landscape structure explains abundance best at small landscape extents (50- or 100-m radius) in the spring and large extents (250- or 500-m radius) in the fall.

Table 2-2. Landscape composition and configuration variables used to represent landscape structure, with descriptions of each and the methods of transformation for regression analyses. Maps from which these variables are derived are adapted forms of the Alberta Vegetation Inventory (see text).

Landscape variable	Description	Transformation
Composition - Deciduous	Percent of the total area covered of any deciduous forest, including *Populus* mixes and birch.	Arcsine square-root of proportion
Composition – All conifer	Percent cover of white spruce, black spruce, jack pine, and any mixed forest containing a conifer component greater than 20%.	Square root of percent
Composition – Young deciduous, harvested	Open stands in early deciduous successional stages following harvesting. Vegetation generally did not exceed 4-m in height	Arcsine square-root of proportion
Composition – Young deciduous, burned	Open stands in early deciduous successional stages following fire. Live vegetation generally did not exceed 4-m in height.	Arcsine square-root of proportion
Composition – Young conifer, burned	Open stands in early softwood successional stages, including burned pine and lowland (mostly black spruce bogs). Vegetation height was low except for snags, and there was little understory growth.	Arcsine square-root of proportion
Configuration – Edge density	The length of edge (m) divided by total landscape area (m^2).	None
Configuration – Largest patch index	The percent of the landscape occupied by the largest patch.	Converted to proportion and squared
Configuration – Mean shape index	Average of: Patch perimeter (m)/sq. rt. of area (m^2), adjusted to a circle shape.	None
Configuration – Patch density	The number of patches in the landscape divided by total area.	Log (base 10)
Configuration – Patch richness density	The number of patch types in the landscape divided by total area.	Square-root of (value + 1)
Configuration – Simpson's Evenness Index	An indicator of the equality of distribution of area among patch types in the landscape.	None

Table 2-3. Local vegetation variables used in analyses, showing which small mammal species models each was submitted to and descriptions of and transformations applied to each.

Vegetation variable	Species model submitted to	Description	Transformation
Aspen trees	*C. gapperi*, *P. maniculatus*	Mean number per plot	Square-root
Birch trees	*C. gapperi*, *P. maniculatus*	Mean number per plot	Double log (base 10) of (value + 1)
Small trees	*P. maniculatus*	Mean number < 15-cm dbh per plot	Square-root
All coarse woody debris	*C. gapperi*	Mean number of pieces per plot	Log (base 10) of (value + 1)
Large coarse woody debris	*P. maniculatus*	Mean number > 15.1-cm dbh per plot	Log (base 10) of (value + 1)
Large snags	*C. gapperi*	Mean number > 15.1-cm diameter per plot	Double log (base 10) of (value + 1)
Shrub cover	*C. gapperi*	Mean percent cover per plot	None
Ground cover	*C. gapperi*	Mean percent cover per plot	None
Shrub species richness	*P. maniculatus*	Total richness for all 3 plots	None
Herb cover	*C. gapperi*	Total score for all 3 plots	None
Grass cover	*P. maniculatus*	Total score for all 3 plots	None
Willow cover	*P. maniculatus*	Total score for all 3 plots	Log (base 10) of (value + 1)
Alder cover	*C. gapperi*, *P. maniculatus*	Total score for all 3 plots	None
Lichen cover	*C. gapperi*, *P. maniculatus*	Total score for all 3 plots	Double log (base 10) of (value + 1)
Blueberry cover	*P. maniculatus*	Total score for all 3 plots	None

Table 2-4. Percentage of the full models for *C. gapperi* and *P. maniculatus* abundance that demonstrate positive or negative associations with landscape heterogeneity. *C. gapperi* abundance is most frequently positively related to heterogeneity when it enters models on the reference study area, while *P. maniculatus* is consistently negatively related to heterogeneity when it is present in models on the burned study area.

Study species	Study area	% with positive association	% with negative association
C. gapperi	Reference	50	18
	Managed	19	13
	Burned	19	25
P. maniculatus	Reference	22	14
	Managed	16	16
	Burned	0	25

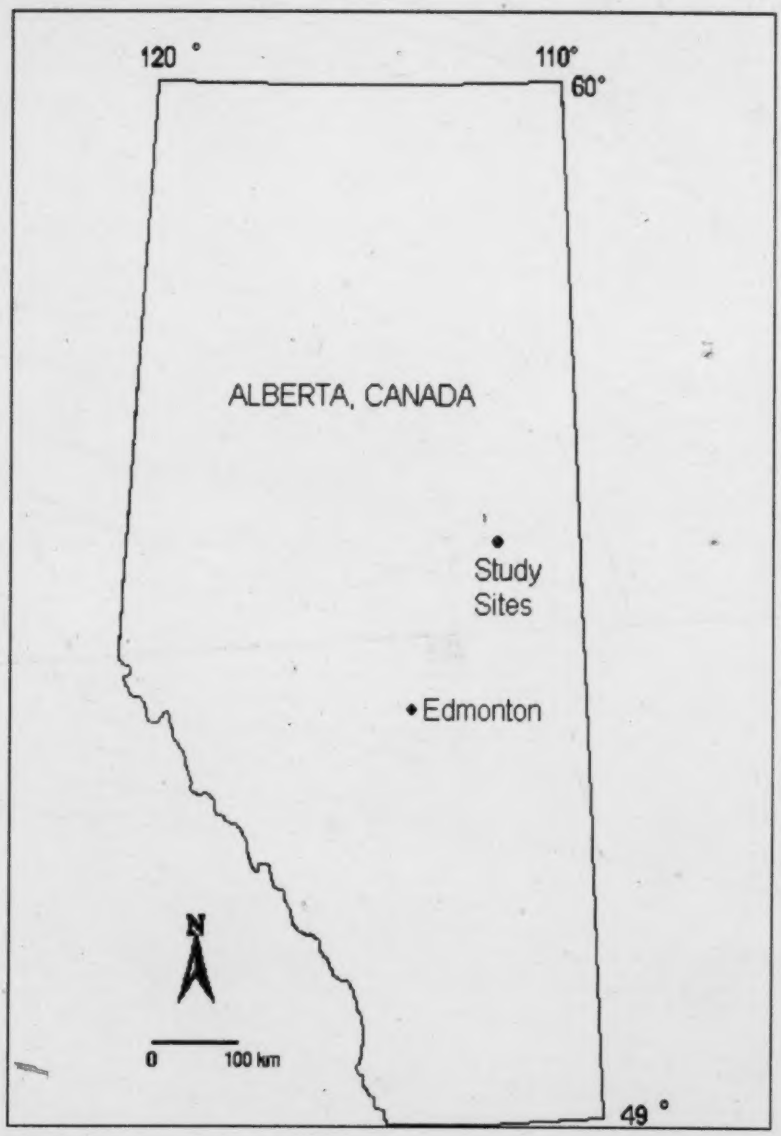


Figure 2-1. Map of Alberta, Canada, indicating the location of study sites about 350 km northeast of the capital city of Edmonton.

2-2a

N
0
1
2
3
4
Kilometres
Deciduous
Conifer
Young (harvested)
Marsh
Water

2-2b

N
0 1 2 3 4
Kilometres
Deciduous
Conifer
Young (harvested)
Marsh
Water

2-2c

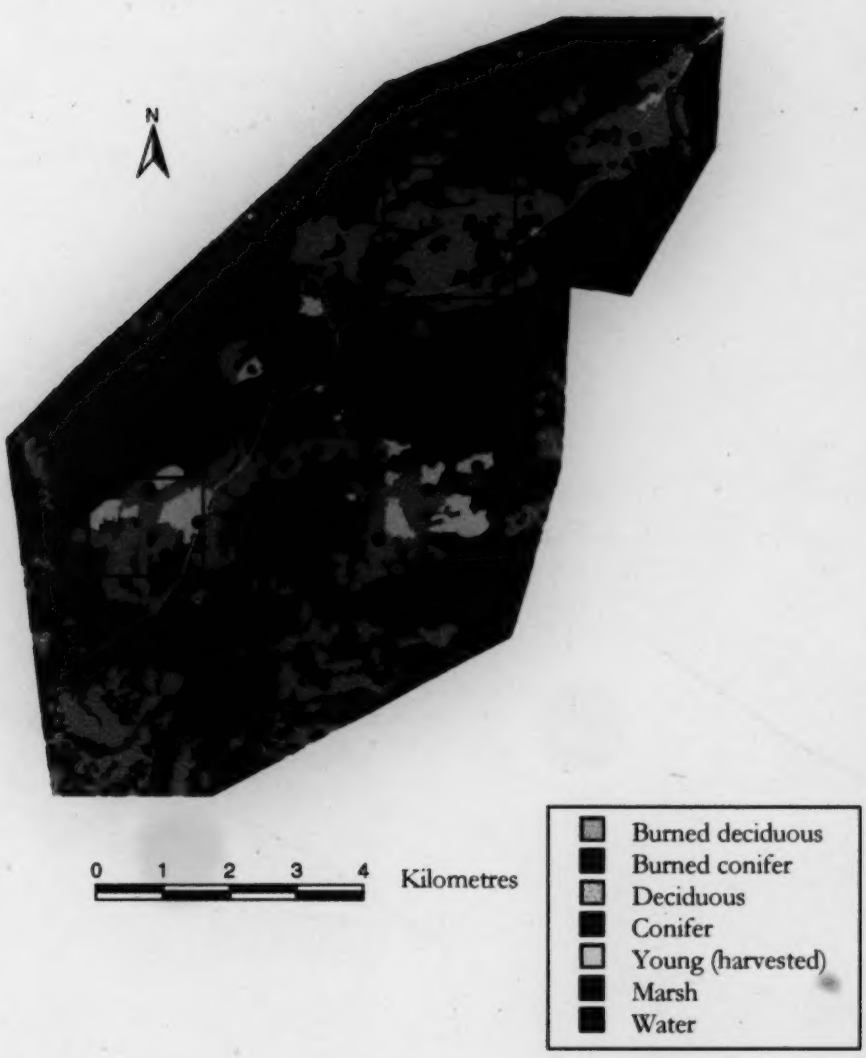


Figure 2-2. Forest vegetation maps of the reference (a), managed (b), and burned (c) study areas. Positions of macro (1000-m grain) grid points and meso (250-m grain) grids are shown in black. X-meso grids are north, Y mesos are south.

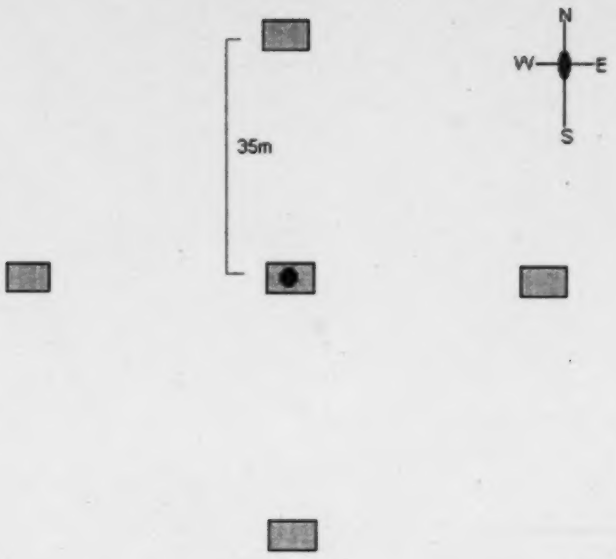


Figure 2-3. Placement of Tin Cat small mammal traps at a grid point. Permanent trap stations were flagged for consistent trapping among sessions.

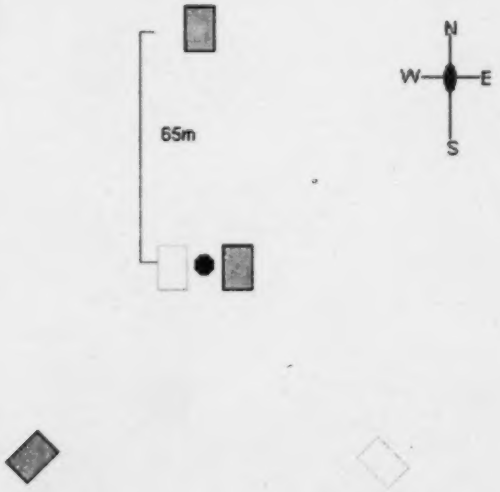


Figure 2-4. Configuration of vegetation sampling plots around a grid point. Plots were 10 by 20 m with the centre plot always sampled (alternately east and west of point centre) and two of the three outer plots chosen systematically. Shaded plots represent an example.

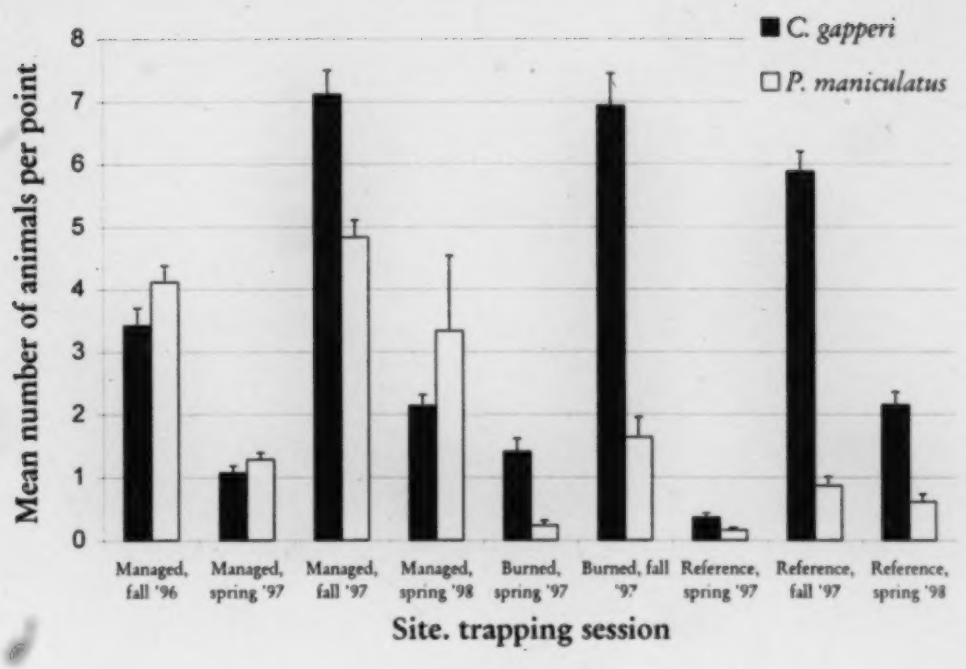


Figure 2-5. Mean number of *Clethrionomys gapperi* and *Peromyscus maniculatus* per sampling point in each area after 2 days of trapping in each session. Error bars show one standard error. Spring abundance was generally lower than fall, particularly for *C. gapperi*. *Peromyscus maniculatus* was found in lower abundance than *C. gapperi* in the reference and burned areas, but was generally higher in the managed area, with the exception of the fall trapping session in 1997.

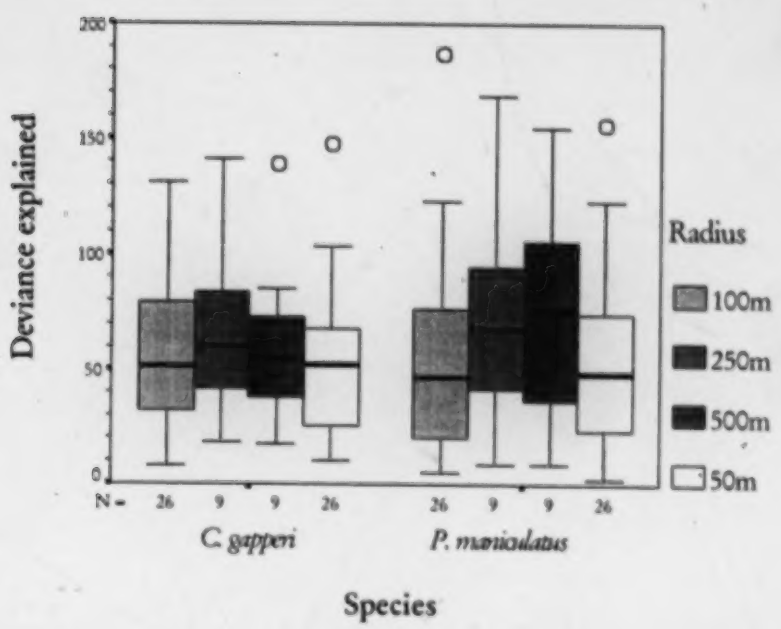
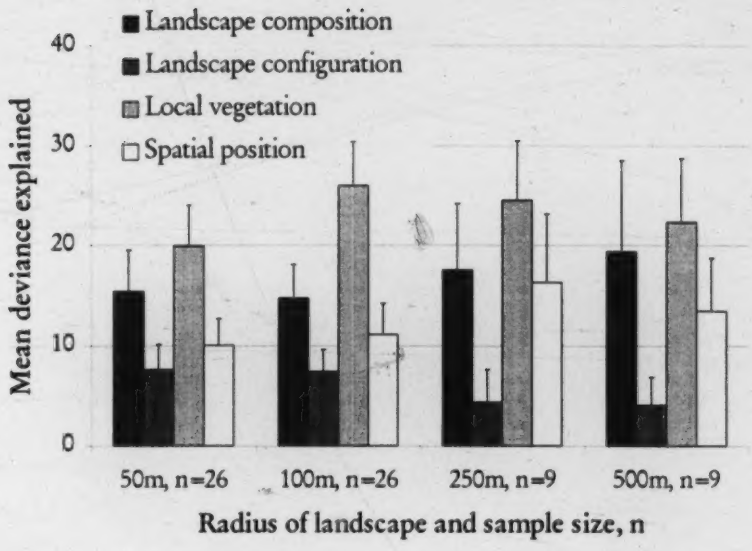


Figure 2-6. Box plot of the deviance explained by full models for both *C. gapperi* and *P. maniculatus*, showing medians (horizontal lines through boxes), 50% interquartile ranges (boxes) and highest and lowest values (whiskers), excluding outliers (indicated by circles). Models explain similar amounts of deviance regardless of landscape extent or species considered.

2-7a



2-7b

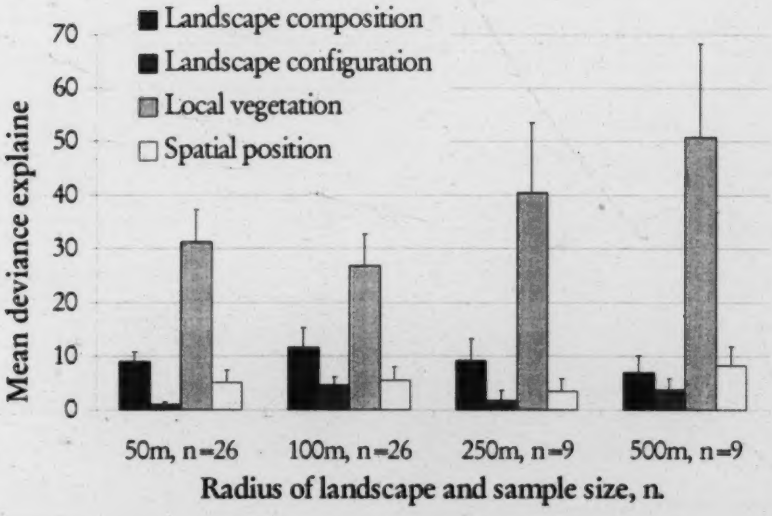
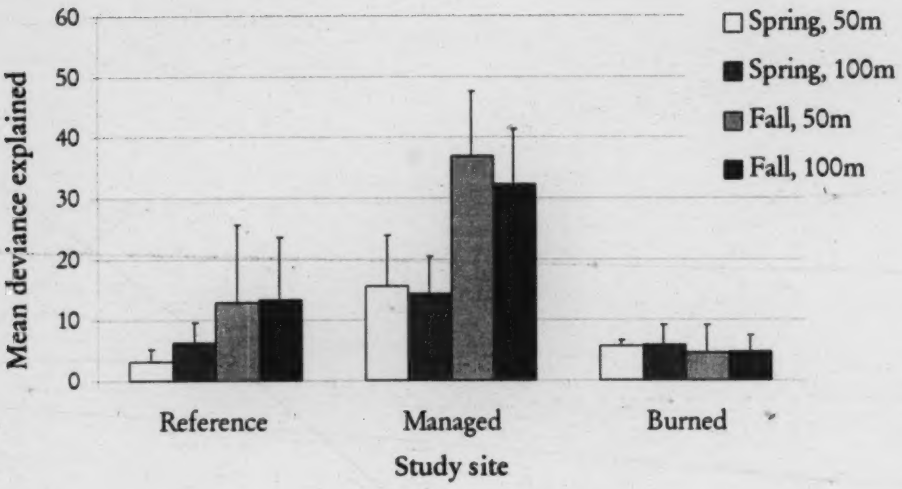
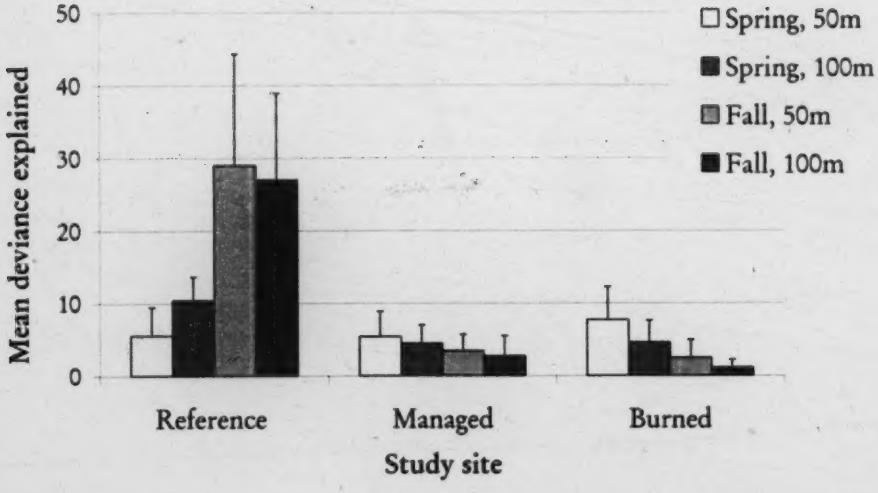


Figure 2-7. Mean deviance explained by each predictor data set at each landscape extent for *C. gapperi* (a) and *P. maniculatus* (b). Error bars denote one standard error. The number of response data sets used to produce each mean (n) is indicated. Local vegetation explained the most deviance, particularly for *P. maniculatus*, followed by landscape composition, spatial position and landscape configuration.

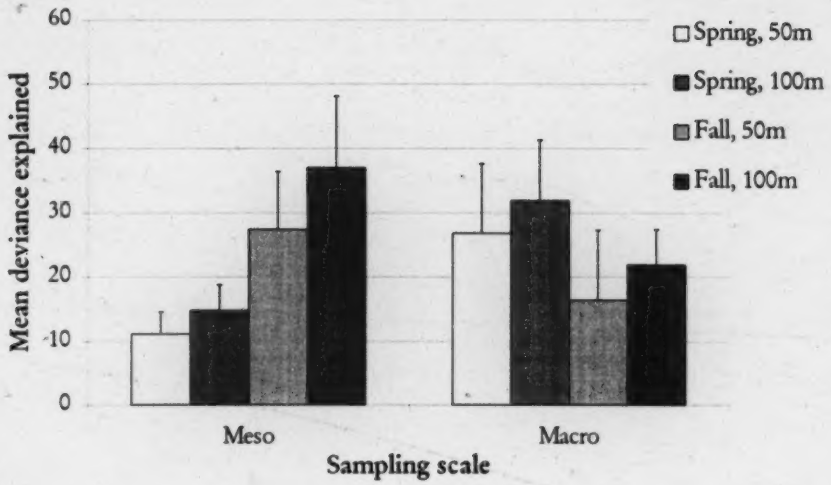
2-8a


Mean deviance explained
60
50
40
30
20
10
0
Spring, 50m
Spring, 100m
Fall, 50m
Fall, 100m
Reference
Managed
Burned
Study site

2-8b


Mean deviance explained
50
40
30
20
10
0
Spring, 50m
Spring, 100m
Fall, 50m
Fall, 100m
Reference
Managed
Burned
Study site

2-8c



2-8d

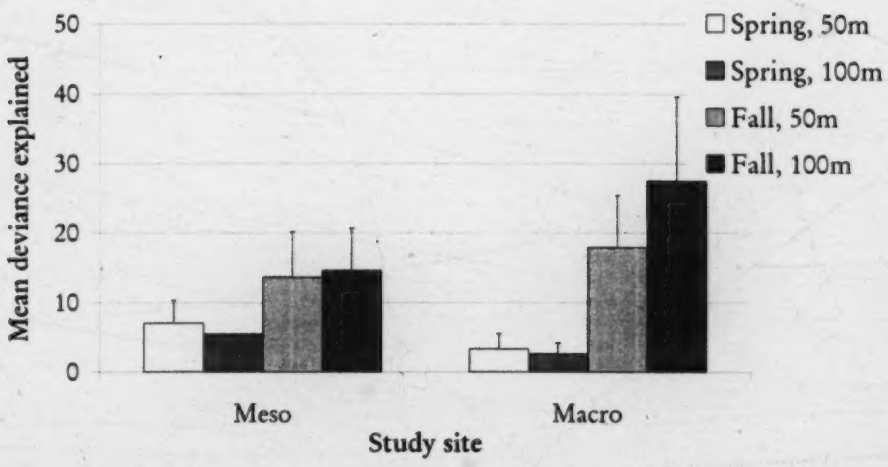
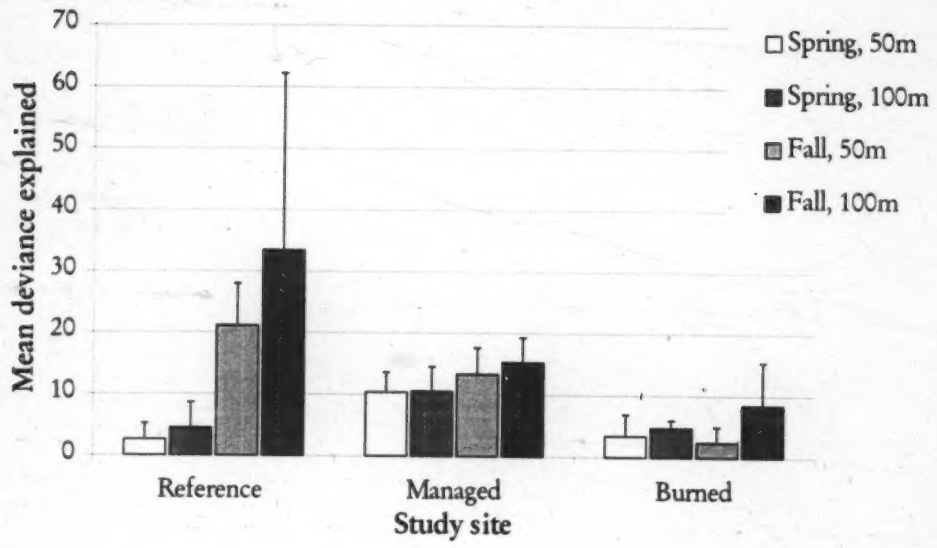
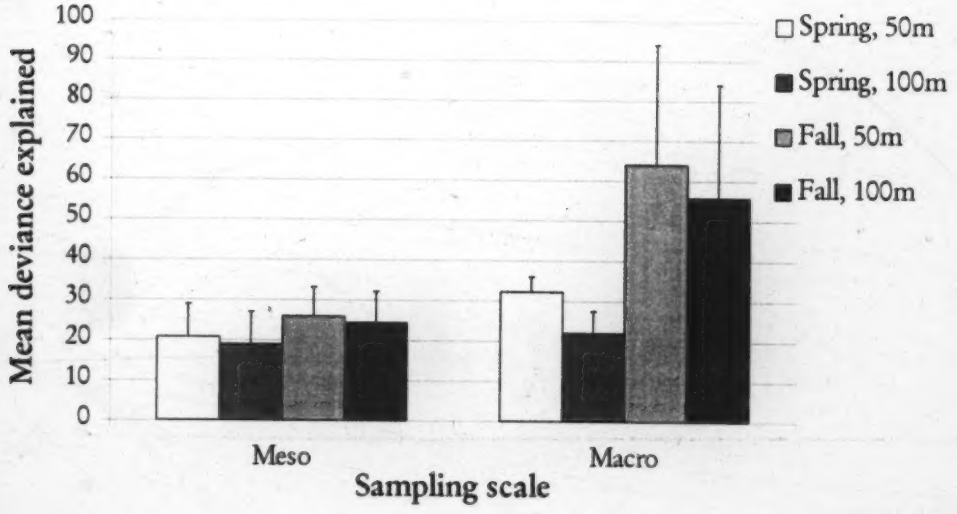


Figure 2-8. Mean deviance in *C. gapperi* abundance explained by landscape composition (a), landscape configuration (b), local vegetation (c) and spatial position (d). Error bars denote one standard error. The amount of deviance explained by landscape composition was always higher in fall than spring and on the managed study area than on others. The deviance explained by landscape configuration was highest in the fall on the reference study area. Local vegetation explained the most deviance in fall on meso grids due to high values in 1996. Spatial position explained little deviance in spring on any study areas, but was an important predictor of abundance in fall, particularly on macro grids.

2-9a


Mean deviance explained
70
60
50
40
30
20
10
0
Reference
Managed
Burned
Study site
Spring, 50m
Spring, 100m
Fall, 50m
Fall, 100m

2-9b


Mean deviance explained
100
90
80
70
60
50
40
30
20
10
0
Meso
Macro
Sampling scale
Spring, 50m
Spring, 100m
Fall, 50m
Fall, 100m

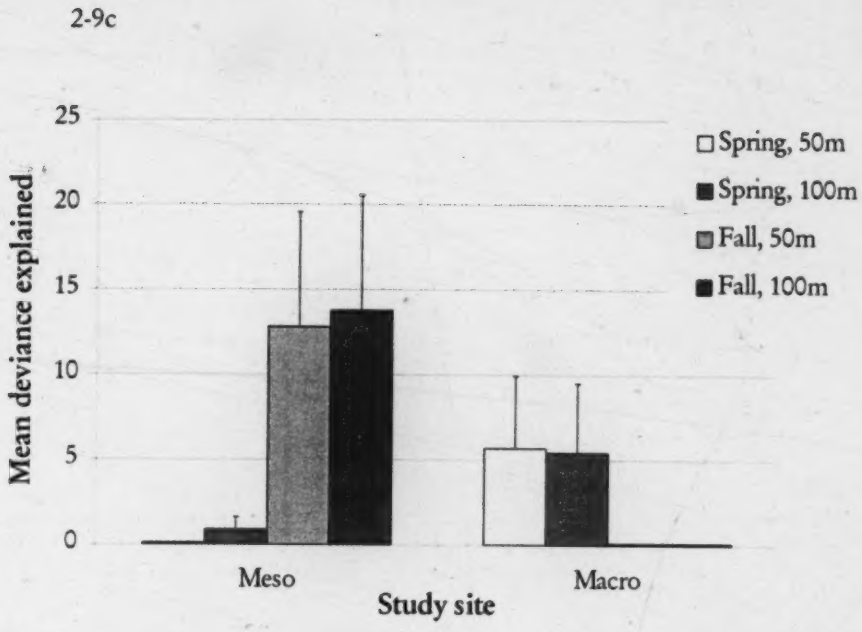


Figure 2-9. Mean deviance in *P. maniculatus* abundance explained by landscape composition (a), local vegetation (b) and spatial position (c). Error bars denote one standard error. Landscape composition explained the most deviance in fall on the reference study area, but was otherwise not a strong predictor of abundance. Local vegetation was a better predictor in fall than in spring on macro grids. Spatial position explained little or no variation in abundance on macro grids, but was a better predictor on meso grids in the fall.

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Appendix 1. Mean and variance of each landscape variable for all grids at all extents.

Grid	Number of points	Extent	% Deciduous mean	% Deciduous variance	% Conifer mean	% Conifer variance
Reference macro	57	50	58.0337	1931.655	38.6265	1957.549
Reference macro	57	100	55.7160	1565.115	37.4325	1511.704
Reference macro	57	250	51.6161	1028.634	38.5146	1045.855
Reference macro	57	500	49.1965	740.583	40.2128	769.104
Reference x-meso	64	50	43.0094	1804.243	52.8795	1885.443
Reference x-meso	64	100	40.6956	1317.876	52.9058	1458.844
Reference y-meso	64	50	36.9277	1669.129	62.8298	1683.109
Reference y-meso	64	100	38.8580	1424.744	60.6206	1443.837
Managed macro	60	50	57.5383	1812.980	24.7438	1489.597
Managed macro	60	100	56.9207	1491.474	24.1645	1252.778
Managed macro	60	250	53.0182	977.544	25.7995	988.782
Managed macro	60	500	51.6832	732.920	27.0065	738.475
Managed x-meso	64	50	82.9787	960.083	3.0087	124.910
Managed x-meso	64	100	81.8442	759.675	3.5291	64.109
Managed y-meso	63	50	67.4716	1662.666	3.6681	195.916
Managed y-meso	63	100	63.3683	1283.459	6.1732	261.993
Burned macro	26	50	45.7573	2147.599	7.6638	410.414
Burned macro	26	100	37.7869	1472.554	7.5312	234.078
Burned macro	26	250	22.5988	654.854	8.9869	266.637
Burned macro	26	500	17.5038	478.600	9.2850	149.932
Burned x-meso	41	50	56.6829	1746.723	19.0061	819.763
Burned x-meso	41	100	56.0980	1384.907	19.1861	645.309
Burned y-meso	9	50	13.1100	884.467	11.3278	1106.117
Burned y-meso	9	100	9.9167	497.938	0.6889	4.217

Grid	Number of points	Extent	% Young Deciduous mean	% Young Deciduous variance	% Young Conifer mean	% Young Conifer variance
Reference macro	57	50	1.4972	32.758	0.0000	0.000
Reference macro	57	100	3.4182	54.552	0.0000	0.000
Reference macro	57	250	3.4402	37.287	0.0000	0.000
Reference macro	57	500	3.7688	32.542	0.0000	0.000
Reference x-meso	64	50	2.5458	172.811	0.0000	0.000
Reference x-meso	64	100	3.4153	157.890	0.0000	0.000
Reference y-meso	64	50	0.0000	0.000	0.0000	0.000
Reference y-meso	64	100	0.0000	0.000	0.0000	0.000
Managed macro	60	50	17.1990	1015.716	0.0000	0.000
Managed macro	60	100	16.5582	748.378	0.0000	0.000
Managed macro	60	250	15.7195	361.171	0.0000	0.000
Managed macro	60	500	12.9723	149.805	0.0000	0.000
Managed x-meso	64	50	12.9031	870.994	0.0000	0.000
Managed x-meso	64	100	13.0269	668.429	0.0000	0.000
Managed y-meso	63	50	28.3603	1579.768	0.0000	0.000
Managed y-meso	63	100	28.6124	1219.162	0.0000	0.000
Burned macro	26	50	17.8277	1334.784	28.6654	1736.438
Burned macro	26	100	21.1088	1077.142	32.5396	1362.651
Burned macro	26	250	25.8819	883.133	37.8165	1026.448
Burned macro	26	500	22.7800	530.345	41.1758	539.854
Burned x-meso	41	50	4.6695	176.469	19.6295	1179.644
Burned x-meso	41	100	4.9173	107.355	19.5059	902.329
Burned y-meso	9	50	75.5411	1655.378	11.3278	1106.117
Burned y-meso	9	100	75.8678	1095.033	12.4789	875.130

Grid	Number of points	Extent	Edge Density mean	Edge Density variance	Largest Patch Index mean	Largest Patch Index variance
Reference macro	57	50	64.8284	6938.224	89.4718	266.717
Reference macro	57	100	79.5086	4751.581	79.6337	357.610
Reference macro	57	250	82.0698	1919.307	62.9435	508.715
Reference macro	57	500	80.5661	1089.576	54.0553	400.862
Reference x-meso	64	50	80.9344	7669.189	85.9780	286.298
Reference x-meso	64	100	91.1542	5085.853	76.9238	380.137
Reference y-meso	64	50	61.3802	5369.982	89.0033	224.831
Reference y-meso	64	100	55.4769	2459.548	82.9977	325.205
Managed macro	60	50	74.4683	8093.287	87.3600	268.852
Managed macro	60	100	83.4768	5382.526	77.3312	454.018
Managed macro	60	250	78.3338	2124.353	62.6505	521.236
Managed macro	60	500	78.9740	924.920	52.1333	437.914
Managed x-meso	64	50	43.4044	4741.410	92.5153	206.227
Managed x-meso	64	100	48.0066	3082.071	87.5164	299.428
Managed y-meso	63	50	56.8617	5151.995	90.8827	200.095
Managed y-meso	63	100	64.5610	2813.581	81.7425	286.896
Burned macro	26	50	68.5608	4634.578	89.3946	227.401
Burned macro	26	100	93.7127	3445.718	73.6073	420.424
Burned macro	26	250	84.9081	1280.121	56.1073	295.352
Burned macro	26	500	83.8250	540.687	41.7981	223.474
Burned x-meso	41	50	97.0788	10364.176	82.6844	368.108
Burned x-meso	41	100	91.8261	5924.049	72.8707	564.518
Burned y-meso	9	50	92.6156	5505.933	83.1333	212.933
Burned y-meso	9	100	80.6056	918.521	70.8922	202.996

Grid	Number of points	Extent	Mean Shape Index mean	Mean Shape Index variance	Patch Density mean	Patch Density variance
Reference macro	57	50	1.1921	0.061	215.5840	9455.553
Reference macro	57	100	1.3119	0.063	86.4461	2338.523
Reference macro	57	250	1.5282	0.043	32.8758	294.863
Reference macro	57	500	1.7404	0.024	18.1163	74.940
Reference x-meso	64	50	1.1880	0.040	230.0061	12057.191
Reference x-meso	64	100	1.3288	0.040	97.9870	3148.152
Reference y-meso	64	50	1.1359	0.028	208.0047	10143.340
Reference y-meso	64	100	1.2508	0.055	71.4917	1258.976
Managed macro	60	50	1.1400	0.027	236.8287	18244.607
Managed macro	60	100	1.2970	0.044	91.7267	2932.450
Managed macro	60	250	1.5007	0.051	31.8292	306.670
Managed macro	60	500	1.6343	0.021	18.7665	70.834
Managed x-meso	64	50	1.1055	0.027	187.9911	8301.433
Managed x-meso	64	100	1.2223	0.049	69.4905	1805.324
Managed y-meso	63	50	1.1521	0.033	205.2317	7160.849
Managed y-meso	63	100	1.2476	0.032	77.1944	1539.628
Burned macro	26	50	1.2050	0.047	241.2512	12226.334
Burned macro	26	100	1.3815	0.046	102.1369	1884.494
Burned macro	26	250	1.5285	0.022	32.2958	184.089
Burned macro	26	500	1.7292	0.013	17.1262	33.918
Burned x-meso	41	50	1.1846	0.035	255.9932	18027.538
Burned x-meso	41	100	1.3024	0.041	97.5437	3680.759
Burned y-meso	9	50	1.1822	0.022	256.0656	16414.745
Burned y-meso	9	100	1.2878	0.012	78.2100	540.276

Grid	Number of points	Extent	Patch Richness Density mean	Patch Richness Density variance	Simpson's Eveness Index mean	Simpson's Eveness Index variance
Reference macro	57	50	202.1104	6406.516	0.2651	0.136
Reference macro	57	100	68.4833	1003.152	0.4402	0.132
Reference macro	57	250	18.6835	56.634	0.5749	0.087
Reference macro	57	500	7.3656	4.756	0.6039	0.039
Reference x-meso	64	50	218.0061	7636.016	0.3606	0.149
Reference x-meso	64	100	76.9905	933.291	0.4953	0.110
Reference y-meso	64	50	192.0047	5201.961	0.2998	0.139
Reference y-meso	64	100	58.9931	462.051	0.4167	0.152
Managed macro	60	50	215.4917	10833.895	0.3138	0.139
Managed macro	60	100	77.3273	1294.618	0.4700	0.142
Managed macro	60	250	19.7970	55.0525	0.6162	0.077
Managed macro	60	500	7.5520	3.093	0.6442	0.048
Managed x-meso	64	50	183.9923	6694.349	0.1831	0.101
Managed x-meso	64	100	59.4917	743.075	0.2880	0.119
Managed y-meso	63	50	203.2011	6683.667	0.2489	0.114
Managed y-meso	63	100	69.0692	964.270	0.4140	0.102
Burned macro	26	50	226.4819	8268.775	0.2669	0.109
Burned macro	26	100	86.1404	1045.396	0.5469	0.121
Burned macro	26	250	21.4650	56.683	0.7277	0.040
Burned macro	26	500	8.5658	7.173	0.7588	0.020
Burned x-meso	41	50	249.7495	16349.029	0.3866	0.146
Burned x-meso	41	100	84.2795	1880.541	0.5083	0.142
Burned y-meso	9	50	241.8289	14128.016	0.4578	0.142
Burned y-meso	9	100	74.6544	511.813	0.7211	0.061

Chapter 3 - Small mammal response to understory patchiness in aspen-dominated forests

Introduction

Understanding the effects of spatial configuration of habitat on animal distribution is an important aspect of landscape ecology. This is because animal movement, and thus any ecological processes linked to it (*i.e.* foraging, dispersal or migration), may be limited or enhanced by landscape structure (Fahrig and Merriam 1994). Animals move through and interact with landscapes at a variety of spatial scales, depending on the species (Milne *et al.* 1992) and ecological process (Bowers and Dooley 1991, Morris 1992) under consideration. The process of dispersal is the one most commonly addressed in landscape ecology, since this often determines size and persistence of isolated populations, such as those created by large-scale habitat fragmentation. Landscape structure at the spatial scale of foraging movements (the extent of which generally coincides with the home range) has received less attention. This may be because conservation issues that sometimes drive research are usually focussed on areas larger than a home range and are addressed at population, rather than individual, levels. Confining landscape research to very large scales is problematic since knowing the effects of habitat heterogeneity on individuals at local scales is important for understanding population-level responses over larger landscapes (Bowers *et al.* 1996).

Landscapes perceived by animals during foraging activity have patches that are defined primarily by resources of varying quality or function and their boundaries are sometimes difficult for humans to delineate. Unless these patches coincide with something obvious to human perceptions (*e.g.* forest remnants in a matrix of disturbance or tall grass in a mowed field), they are rarely mapped and studied. Patch types defined by researchers (usually from land cover maps derived from aerial photography) have proven relevant at dispersal scales for many animals, perhaps due to a coarser scale of habitat selection during this process. But there are fewer instances where our patch definitions have revealed meaningful relationships at home range scales. The landscape composition of home ranges has been shown to be important for flying squirrels (Mönkkönen *et al.* 1997), northern spotted owls (Ripple *et al.* 1997), Mexican spotted owls (Grubb *et al.* 1997), moose (Forbes and Theberge 1993) and caribou (Bradshaw *et al.* 1995). It should not be surprising that the

amount of good or bad habitat in a home range area affects the probability of its occupancy or the success of its occupants.

The effects of patch configuration or heterogeneity within home ranges is a more interesting issue for landscape ecologists since use of available resources may be affected by their spatial configuration. However, there have been fewer studies in this area. Habitat diversity within home ranges is probably the most studied aspect of configuration. Coulson (1993) showed that grey kangaroos in Australia require a diversity of patch types within their home ranges, as different patches are used for different things at different times (*i.e* sleeping, foraging, travelling). Similarly, red foxes (Lucherini and Lovari 1995) and black-tailed jackrabbits (Knick and Dyer 1992) are positively associated with habitat heterogeneity within home ranges. Though diversity of patch types was important in these studies, it is unknown whether their spatial arrangement contributed to home range quality. Like the aforementioned species, primates use different patch types in their home ranges. Garber (1990) documented goal-directed foraging in tamarins where use of a number of different food trees each day (resource patches) was based on the proximity of trees to each other. Barton *et al.* (1992) showed that baboons used feeding sites within home ranges that were closest to nest sites or water sources. These studies show that animals do respond to habitat configuration at a small scale, but only one (Oksanen *et al.* 1992) demonstrated how landscape configuration may cause differential use of eligible home ranges. Oksanen *et al.* (1992) suggest that predatory strategies are dependent on average patch size within home ranges, and that predator densities on a landscape increase when productive habitat exists in larger patches.

All of these studies are similar in that the species considered are relatively large and/or volant and are associated with large-scale (human-detectable) habitat types. There are no studies to my knowledge examining home range landscape structure on very small, ground-dwelling mammals such as voles and mice, even though there is much literature on landscape effects on this group at population scales. Small mammals may be one of the simplest groups with which to address changing associations with landscape structure at different spatial scales, since distributions are easy to measure, and landscapes are relatively small, even at dispersal scales. I had abundance data for two species of small mammals, *Clethrionomys gapperi* and *Peromyscus maniculatus*, at sampling locations where forest landscape structure was measured for a larger-scale landscape ecology study on these species (Chapter

2). During field work for that study, it was noted that animal abundance at multiple-capture trap stations seemed to be associated with proximity of shrub patches when understory was otherwise fairly open. I became interested whether the amount and configuration of different patches around trap stations had any effect on the number of animals caught there. I also wondered if understory landscape structure might be a better predictor of small mammal abundance than the more recognizable structure of landscapes defined by forest stands. The present study was conducted to test these ideas by addressing two specific questions:

1. Can variation in small mammal abundance among individual trap stations be explained by differences in understory composition or configuration surrounding them?
2. How does configuration of understory vegetation affect small mammal abundance relative to forest stand landscape structure?

Materials and methods

Study Areas

I used data from thirty-five sampling points from systematic grids used in another study on forest stand-level landscape effects (Chapter 2). These grids were located at approximately 55°N and 112°E in the mixed-wood boreal forest of northeastern Alberta, Canada (Figure 3-1). Points were at least 250 m apart and the area from which they were selected covered about 250 ha (composed of two sets of points about 6 km apart). All points were located in mature aspen (*Populus tremuloides*) forests, but there were essentially two types of aspen community included. The first community type was represented by 23 points characterized by tall aspen trees, with patches of beaked hazel (*Corylus cornutus*), rose (*Rosa* sp.) or herbs (*Sarsparilla* sp. or fireweed) dominating the understory. Ground cover at these points was almost always composed of low-growing herbs and rarely *Rubus pubescens* or grasses. Some of these points contained small groves of white spruce under which there was little or no shrub or ground cover. The other aspen community included 12 points characterized by widely spaced, stunted aspen trees mixed with jack pine. These points had a relatively sparse understory, with clumps of alder (*Alnus* sp.) and individual aspen suckers dominating the shrub layer. Lichen (*Cladina* sp.), mosses and *Vaccinium* sp. formed the ground cover in these sites. Some understory patches in both community types resulted from small linear

disturbances such as cutlines or forest harvesting adjacent to points. Tall grasses and herbs, aspen suckers and raspberry bushes (*Rubus* sp.) dominated these areas.

Study species

The species studied were *Clethrionomys gapperi* (red-backed voles) and *Peromyscus maniculatus* (deer mice). *C. gapperi* has been shown to be associated with ground and shrub cover, birch and herb abundance and coarse woody debris in aspen forests of this region (Roy *et al.* 1995, Chapter 2). It feeds on green vegetation, seeds, nuts, roots, fungi and insects (Forsyth 1985, Burt and Grossenheider 1980, Whitaker 1980). Adults generally occupy home ranges around 0.1 to 0.5 ha (Burt and Grossenheider 1980, Bondrup-Nielsen 1987). *P. maniculatus* in the region are associated with birch, alder, willow, *Vaccinium* sp., grass, shrub species richness, small trees and large downed woody debris (Roy *et al.* 1995, Chapter 2). Food resources are primarily seeds, nuts and invertebrates (Forsyth 1985, Burt and Grossenheider 1980, Whitaker 1980). Home ranges are reported from 0.2 to 2.1 ha (Burt and Grossenheider 1980).

Small mammal abundance

Live trapping at each sampling point assessed relative abundance of small mammals. Five Victor Tin Cat multiple-capture live traps were set at each point, one at the centre and one approximately 35 m out in each cardinal direction (Figure 3-2). The numbers of individuals caught in each trap, as well as the total number of animals caught at a point, were used as response variables for the analyses. Traps were prebaited at trap stations with oats and sunflower seeds for 2-7 nights before trapping began and were checked once daily for 2-3 days during trapping. Data from three live-trapping sessions were collected. The first session (May 1 to June 16, 1997) used three consecutive nights at each point. The second (Aug. 24 to Oct. 6, 1997) and third (May 1 to June 6, 1998) sessions used a two trap-night system. Upon capture, new individuals were sexed, weighed and marked using an aqueous picric acid solution. Marking prevented previously caught individuals from being recounted in subsequent trapping nights. In order to be sure that spring abundance estimates were not unequally biased by recruitment, juveniles were excluded.

Landscape composition and configuration

Landscapes were mapped in 5 by 5-m plots covering 0.81 ha around a point centre (50-m radius). Vegetation was quantified in three vertical strata and the presence or absence of coarse woody debris and trap stations was noted in each plot. The strata included tall shrubs (1.3 m to 4 m in height), medium shrubs (0.3 to 1.3 m in height), and ground cover (<0.3 m in height). For each stratum, observers recorded a categorical score for cover of all vegetation and the dominant species of plant. Cover scores were labeled 1-4, with 1 for <1% cover or <5 stems, 2 for 1-20% cover, 3 for 20-50% cover, and 4 for >50% cover. All combinations of cover score and dominant species were reduced to a smaller number of possible patch types, based on the cover of structurally distinct types of vegetation as well as the amount of coarse woody debris (see Table 3-1 for descriptions of each patch type). Patches with coarse woody debris present were not distinguished according to the type of vegetation due to the assumption that dead wood took precedence over vegetation cover type for small mammals at this scale. Each plot was given a number from 1 to 22 that represented its patch type. This information was used to create a map coverage in ARC/INFO and ARCedit (Environmental Systems Research Institute Inc. 1997) geographic information systems (GIS), with adjacent plots merged when the patch types were the same number. Figure 3-3 shows an example of an understory map produced by this method.

FRAGSTATS software (McGarigal and Marks 1994) was used to generate descriptive variables for composition and configuration of the understory in the entire 50-m radius landscape, and in circles of 12.5-m radius around each trap. 12.5 m was chosen to ensure that landscape structure around neighbouring traps were independent (non-overlapping) since traps were occasionally closer than the intended 35 m. This radius gave landscapes of 0.05-ha extent, which is probably less than the actual home range areas of the study species. However, this area did provide independent samples of understory landscape structure within home ranges that contained traps. Percent cover of each patch type from these analyses was used to remove effects of local vegetation composition to allow for identification of additional effects of spatial arrangement, or configuration. Landscape structure at the forest stand level was similarly measured within 50 m of point centres based on Alberta Vegetation Index forest cover maps prepared in GIS (see Chapter 2 for more details). This allowed comparisons of response to landscapes defined at very different grains.

Due to the geometric shapes of patches in understory landscapes (a result of using square plots to map vegetation), configuration variables describing edge density or edge to area ratios were not accurate and not comparable due to the changing magnitude of the bias with patch size. Therefore, these indices were not used for landscape analyses. The indices that were considered included: largest patch index (percent cover of the largest patch), number of patches, patch richness (number of different patch types), and Simpson's evenness index (approaches one as area becomes more evenly distributed among patches in the landscape). These variables reflect the relative degree of heterogeneity in the landscapes and should not be biased by the mapping method.

Spatial position

Spatial population processes and the resultant spatial autocorrelation were considered sources of variation due to the proximity of sample points and traps. Using geographic position of individual traps and points (depending on the level of analysis) as explanatory variables controlled for this variation. Spatial data for points were collected in the field using Trimble Geoexplorer global positioning system (GPS) units. Bias in satellite information used to calculate spatial position was corrected using base station data from Alberta-Pacific Forest Industries Ltd. The coordinates of peripheral trap stations were calculated from the central points based on their positions recorded on understory maps. Spatial data included Universal Transverse Mercator (UTM) coordinates, x (Eastings in metres) and y (Northings in metres), and seven other terms from a cubic trend surface regression of the form (after Legendre 1990, Borcard *et al.* 1992):

$$Z = ax + by + cxy + dx^2 + ey^2 + fx^2y + gxy^2 + hx^3 + iy^3$$

By considering these terms as predictors in regression, spatial structure or autocorrelation in east-west (x, x^2, x^3), north-south (y, y^2, y^3) and diagonal (xy, x^2y, xy^2) directions could be detected and its effects partitioned from other variables of interest.

Statistical analysis

Regression analyses were used for each species in each trapping period to determine what factors explained variation in abundance. Count data of both species was highly skewed, and did not satisfy the least-squares assumption of a normal distribution of errors. Therefore,

generalized linear models (GLMs) were used (specifications of models: quasi-likelihood family with log link and mean variance functions; S-Plus version 4.5, Mathsoft Inc. 1998). Results from GLMs are given in terms of null and residual deviance. Deviance measures the amount of scatter around a linear model, incorporating dispersion and specified link and variance functions (Green and Silverman 1994). The null deviance is based on a null model of "response = 1". Residual deviance is the sum of deviance increments for each observation, and may be interpreted as the variation that is not be explained by the model.

The number of predictor variables available for these regressions was high, therefore GLMs were conducted using forward selection for variable entry. This procedure (using the "step" command in S-Plus (Mathsoft 1998)) involves fitting predictor variables one by one to a model, and calculating Akaike's Information Criterion (AIC, Akaike 1973) for each new potential model and the original. The AIC is a penalized version of the log-likelihood function that can be used to evaluate the fit of a model (Akaike 1973, McCullagh and Nelder 1989). The variable that produces the model with the lowest AIC statistic (provided it is lower than the original) is added and the process is repeated, alternately adding the remaining variables to this new model. When no variables can add significantly to the model (as tested by the AIC), the procedure ends.

Variation in abundance per trap station for each species from each trapping period was partitioned among four sets of predictor variables: abundance of the other species, spatial position, understory composition and understory configuration within 12.5 m of traps. Abundance of the other species was included in trap level analyses since the presence of that species in a trap may have precluded its entry by the other species. Forward selection GLMs with variables submitted from all predictor data sets were conducted for each small mammal data set to compute the total deviance explained by all the predictors combined. To determine what fractions of variation were explained by each predictor data set independent of all others, partial regression techniques were used as described by Legendre and Legendre (1998, pg. 532). For each predictor data set, the variable(s) representing that set was removed and the model run again including only the other variables from the previously calculated full model. The difference between the residual deviance of the full and partial models gave the amount of deviance explained by the removed variable(s) independent of the other data sets. This procedure was repeated for each predictor data set that was represented in the full model.

To compare response to understory and forest landscape structure, the above procedure was used, but with the total number of each species caught in all five traps per point as response variables, and spatial position, understory composition and landscape structure within 50 m as predictors. This analysis was done twice, once with landscape structure defined by understory configuration, and once with it defined by forest stand configuration and composition from AVI maps. Comparison of the deviance explained by landscape structure in these two analyses was used to assess whether small mammals responded more to understory or stand-level landscapes.

Results

Small mammal abundance

Data from 1225 trap-nights were used for these analyses. The total number of *C. gapperi* caught was 321, and the total for *P. maniculatus* was 237. Many traps never caught animals, while the maximum number of individuals caught per trap was seven (occurring in *C. gapperi* in fall 1997). The total number of each species at a point ranged from zero to 22 for *C. gapperi* and zero to twelve for *P. maniculatus*. Abundance was generally much lower for both species in spring compared to fall, with a number of spring zero points becoming occupied by the fall trapping session.

Partitioning variation in trap abundance

The amount of deviance explained in species abundance at a trap varied with species and trapping session. Full models had explained deviances ranging from 27.13 to 92.45 (Figure 3-4). Abundance of the other species (except for spring 1997) or understory composition (Figure 3-5) explained much of this variation. *C. gapperi* was always negatively associated with the amount of dense rose or raspberry shrubs in herbaceous communities (patch type 16; Table 3-1). In spring 1997, there were positive associations with sheltered coarse woody debris and *Ledum groenlandicum* in lichen communities (patch types 10, 1 and 5 respectively; Table 3-1). In fall 1997 and spring 1998, abundance was negatively associated with the absence of cover in lichen areas (patch type 7; Table 3-1). In fall 1997, the relationship to coarse woody debris over lichen was slightly negative, and in spring 1998 there was a negative relationship with dense shrubs over herbs (patch types 10 and 17; Table 3-1).

P. maniculatus was related to a number of understory patch types in spring 1997. Abundance increased with sparse shrub cover in herbaceous communities, unless the shrubs were clumping species like alder [patch types 12 (negative), 13, 20 and 15; Table 3-1]. However, high shrub cover and sheltered coarse woody debris were favored in lichen areas (patch types 1 and 10; Table 3-1). Fall 1997 and spring 1998 both showed negative associations with clumped shrub species over lichen, and positive associations with clumped shrubs and rose or raspberry over herbs (patch types 4, 15 and 16 respectively; Table 3-1). In spring 1998, *P. maniculatus* also responded positively to single-stemmed shrubs and negatively to *L. groenlandicum* over herbs (patch types 14 and 18; Table 3-1).

Configuration of understory landscapes substantially contributed to models of abundance only for *P. maniculatus* in spring and fall 1997, when patch richness and Simpson's Evenness Index (fall only) were negatively related to abundance. Spatial structure in abundance patterns was only evident in spring 1997. *C. gapperi* abundance increased in an east-west direction while *P. maniculatus* increased from south-west to north-east.

Partitioning variation in point abundance

When abundance estimates for all traps per point were pooled, the influence of understory configuration for *P. maniculatus* in spring 1997 and the east-west spatial structure for *C. gapperi* in spring 1997 essentially disappeared (Figure 3-6). Point-level models explained less total variation than trap-level (Figure 3-4), whether using understory or stand-level landscape structure.

When point abundance was modeled against understory landscape structure, understory composition was the best predictor data set for both species. *C. gapperi* was always positively related to tall herbs with shrubs in herbaceous communities (patch type 12; Table 3-1). In both 1997 sessions, it was also positively associated with exposed coarse woody debris over herbs (patch type 22; Table 3-1). In spring 1998, abundance was negatively related to tall herbs alone in herbaceous areas (patch type 13; Table 3-1).

P. maniculatus abundance was positively related to single-stemmed shrubs in herbaceous communities in both spring sessions (patch type 14; Table 3-1). It was also positively related to sheltered coarse woody debris over lichen in spring 1997 and negatively related to open herbaceous areas in spring 1998 (patch types 10 and 20; Table 3-1). In fall

1997, abundance increased with clumped shrubs over herbs, but decreased with these species over lichens (patch types 15 and 4, respectively).

Landscape structure at the forest stand level was a better predictor of abundance than configuration of understory patches for *C. gapperi*, and the effects of understory composition often changed due to the inclusion of forest variables in models (Figure 3-6). This species was positively related to open canopy stands in all sessions, but understory composition had no effect in spring 1997, and only a slight effect in other sessions. Abundance increased with the amount of tall herbs and shrubs in fall 1997 in herbaceous communities and with tall herbs only in spring 1998 in lichen areas (patch types 12 and 2; Table 3-1).

P. maniculatus only responded to forest stand structure in spring 1998, when abundance increased with open and deciduous habitat and with the number of patches in the landscape. Understory composition was a more important predictor in these analyses. Abundance always increased with single-stemmed shrubs in herbaceous communities (patch type 14; Table 3-1). It was also positively related to the amount of sheltered coarse woody debris in lichen communities in spring 1997 (patch type 10; Table 3-1) and tall herbs and sheltered coarse woody debris over herbs in the fall (patch types 13 and 21; Table 3-1). Abundance in spring 1998 was negatively associated with tall herbs in lichen areas (patch type 1; Table 3-1).

Discussion

Composition and configuration of understory vegetation at small spatial extents was expected to contribute to the quality of an area as a home range for small mammals. The best regression models of abundance were always at the trap level (*i.e.* 12.5 m around trap stations). Initially, one might suspect that this reflects closer associations with landscape structure at this smaller extent. Partitioning variation provided an objective way to test this idea. Landscape structure and spatial position had comparable effects at trap and point levels (Figures 3-5 and 3-6), but the abundance of the other species at the trap station was an important predictor at the trap level that was not included in point-level analyses. It was the additional effects of this variable that caused trap-level regressions to explain more deviance than point-level models.

Other species abundance was not submitted to point level regressions because there were no strong negative correlations between the point estimates of the two species in preliminary analyses [except for a statistically, but perhaps not biologically, significant coefficient for spring 1998 (Spearman's $\rho = -0.34$, $p = 0.05$)]. The absence of strong correlations at the point level suggests that interspecific effects are very localized, but habitat and landscape associations may be invalid if the study species avoid each other in traps. This is because abundance estimates will be a reflection of the first animal to get to the trap and not a true representation of response to local or landscape conditions outside. There were instances when both species were caught at the same trap station (36 out of 230 where animals were present). This is not a high percentage (16%), but may be frequent enough to negate the idea of trap avoidance. However, the absence of an 'other species' effect in spring 1997 tends to suggest that avoidance could be an issue, but that it is overcome when trapping over longer periods (3 versus 2 trap nights) by providing more time for different individuals to access traps.

Separation of the two species in space could also explain the negative associations seen at trap levels. This separation may have been caused by competitive exclusion from home ranges. Competition would be more severe in times of high densities. The amounts of deviance explained by other species abundance in these analyses are proportional to overall abundance (there were 360 animals in fall 1997, followed by 138 in spring 1998, and 60 in spring 1997; compare to 'other species' deviance in Figure 3-5), offering support for this idea. However, Grant (1970) showed, through behavioural observations in experimental arenas, that *C. gapperi* and *P. maniculatus* are no more aggressive towards each other than among themselves. There is some evidence from sagebrush prairie habitats though (O'Farrel, 1980) that *P. maniculatus* tends to be spatially segregated from other rodent species. Another alternative is that resource partitioning may be driving the trap-level spatial separation since different understory vegetation was associated with the two species during all sessions.

When considering local landscapes immediately surrounding traps, *C. gapperi* numbers decreased with the amount of rose or raspberry bushes. These are very dense and complex shrubs, with little herbaceous growth underneath. Therefore, this patch type likely provides little food for this species since it eats primarily herbaceous material. Vickery *et al.* (1989) also showed a decrease in abundance for *C. gapperi* with increasing shrub cover in

Manitoba. However, studies by Roy *et al.* (1995) and Krefting and Ahlgren (1974), showed positive relationships with shrub cover, which was also demonstrated in the present study by negative associations with the amount of open area around a trap. It is likely that some intermediate level of cover is necessary within home ranges, where there is a balance between protection from predators and productivity of herbaceous ground cover. Positive associations with coarse woody debris and *L. groenlandicum*, as were seen in this study, have been documented elsewhere (Morris 1984, Morris 1996). Coarse woody debris has been associated with small mammal abundance in a number of other studies (Morris 1983, Carey and Johnson 1995, Roy *et al.* 1995) and is used for cover during travelling (Bondrup-Nielsen and Karlsson 1985), so its inclusion in these models was expected.

P. maniculatus has been negatively associated with dense shrub cover in other studies (Miller and Getz 1977, Parren and Cappen 1985) and this was generally true at the trap level in this study, unless the dominant species was *Alnus* sp. or *Salix* sp. growing over herbs (patch type 15). The shrub species that dominated this patch type was alder, and it was generally only present in lichen-dominated communities. When herbs were underneath alder in these forests, it was an important patch type, likely for both cover and food. Coarse woody debris also likely provides an important source of cover in these communities. Conversely, when alder was over lichen grond cover, there was a negative association with *P. maniculatus* abundance. This may be an indirect effect of interspecific avoidance, since *C. gapperi* was negatively associated with open areas in lichen communities and was often observed in traps near alder or retreating under alder bushes in these areas (personal observation).

Total *C. gapperi* abundance at a point was consistently associated with cover of simple shrubs and tall herbs, and also with coarse woody debris in most sessions. These larger scale associations represent an average of more localized responses and reveal general stand characteristics that support higher numbers. It also likely reflects the positive association with open-canopy habitat that was seen in the stand-level analyses, since tall grasses, herbs and shrubs frequently dominate these patches. The fact that understory composition has very little effect on abundance in stand-level analyses supports this idea.

The positive association between *P. maniculatus* and open or sparsely vegetated patches at a trap level in herbaceous communities was lost when considering total point abundance related to landscape structure within a 50-m radius. Abundance was instead

associated with single-stemmed shrubs, primarily beaked hazel, as are common these communities. Patches of open understory were relatively rare compared to dense shrubs in these forest types, and it appears as though *P. maniculatus* may use these areas at a large scale, but then be restricted to more open patches at a finer scale within them. However, the variability in the amount of exposed herbs was much higher at a trap level (variance = 313.8) than at a point level (variance = 147.6). This was because the smaller landscapes measured around individual traps were more likely to have open patches that covered the full range of 0 to 100% composition. The effects of open patches may only have been detected at the trap level because of this statistical difference, since greater variance and larger sample sizes can improve the ability to detect relationships through regression. Variance was equal for coarse woody debris over lichen (≈ 57) at both trap and point scales, and this patch type was positively associated with abundance in both cases. Coarse woody debris is likely so important in the lichen communities that it is considered at both dispersal and home range scales during habitat selection.

In general, trap-level response to spatial structure of habitat at very local scales around traps seems to result primarily from cover and feeding requirements, as one would expect within home ranges. However, these associations change with extent, indicating that different processes involving a different type of habitat assessment are producing the patterns. At the 50-m extent, this process may be dispersal or predation, since these occur at larger spatial scales.

Patch diversity, a function of both composition and configuration, has been positively associated with a number of species. Landscape complementation occurs when a species requires different patches for different resources within a home range (Dunning *et al.* 1992). This process explains the positive relationships with patch diversity in home ranges for grey kangaroos (Coulson 1993), red foxes (Lucherini and Lovari 1995) and primates (Garber 1990, Barton *et al.* 1992). Both *C. gapperi* and *P. maniculatus* consume a fairly wide variety of foods, so diversity of understory resources within a home range might be favoured. However, no strong associations with understory heterogeneity were found for either species. There seems to be no strategy of maximizing the diversity of resources (as measured by understory patch types) within a home range for either species. This may be because the resources consumed in this region are very stable and individuals do not require alternate food reserves. It could also be that the patch delineation used in this study did not

accurately represent the patch types identified by the species. Though there were some general associations with composition of some patch types, there was still a lot of variability in response and the deviance explained was relatively low. This suggests that these patch types may only approximate the real perceptions of the species. The use of 5 by 5-m vegetation plots could also be responsible for the minimal understory landscape effects, since this resulted in a fairly coarse resolution for mapping in an area where patches may be as small as a metre across. Configuration variables suffered the most from this loss of resolution and this may be why there were such small effects of these in regressions.

Conclusions

Understory landscape composition is important for predicting small mammal abundance at traps and at points consisting of trap arrays. There is evidence that small mammals respond to different types of understory vegetation at different scales, perhaps reflecting multi-scaled criteria for habitat selection due to the occurrence of different spatial processes at different scales (*i.e.* foraging and dispersal). Understory landscape configuration is a weak predictor of small mammal abundance, perhaps due to problems with mapping resolution and patch definition. However, stand-level landscape structure is fairly important for *C. gapperi* abundance, which increases with the amount of open canopy habitat in the landscape. Spatial position of trap stations and points was of limited utility in explaining variation in abundance for either species. Finally, there is evidence for spatial separation of these species at the trap level, either due to resource partitioning or social interactions causing trap avoidance or competitive exclusion. The present data and analyses cannot isolate the cause of this fine scale spatial separation, but does warrant further investigation.

Table 3-1. Descriptions of twenty-two patch types defined in understory landscapes. Cover classes and species composition for each stratum for each patch type is given. Cover classes 1-2 represent less than 20% cover, while 3-4 represent greater than 20% cover. Single-stemmed shrubs include any structurally simple species and tree saplings. Clumped shrubs include *Alnus* sp. (alder), *Salix* sp. (willow) and *Betula glandulosa* (bog birch).

Patch code	Woody debris cover	Ground cover	Ground species	Medium shrub cover	Medium shrub species	High shrub cover	High shrub species
1	1-2	1-4	Lichen, moss, *Vaccinium* sp.	3-4	Grass, herbs	3-4 1-4	Anything clumped shrubs
2	1-2	1-4	Lichen, moss, *Vaccinium* sp.	3-4	Grass, herbs	1-2	Anything but clumped shrubs
3	1-2	1-4	Lichen, moss, *Vaccinium* sp.	3-4	Single-stemmed shrubs	1-4	Anything
4	1-2	1-4	Lichen, moss, *Vaccinium* sp.	3-4	Clumped shrubs	1-4	Anything
5	1-2	1-4	Lichen, moss, *Vaccinium* sp.	3-4	*Ledum groenlandicum*	1-4	Anything
6	1-2	1-4	Lichen, moss, *Vaccinium* sp.	1-2	Anything but clumped shrubs	3-4 1-4	Anything Clumped shrubs
7	1-2	1-4	Lichen, moss, *Vaccinium* sp.	1-2	Anything but clumped shrubs	1-2	Anything but clumped shrubs
8	1-2	1-4	Lichen, moss, *Vaccinium* sp.	1-2	Clumped shrubs	3-4 1-4	Anything Clumped shrubs
9	1-2	1-4	Lichen, moss, *Vaccinium* sp.	1-2	Clumped shrubs	1-2	Anything but clumped shrubs
10	3-4	1-4	Lichen, moss, *Vaccinium* sp.	3-4 1-4	Anything Clumped shrubs	1-4	Anything
11	3-4	1-4	Lichen, moss, *Vaccinium* sp.	1-2	Anything but clumped shrubs	1-2	Anything but clumped shrubs
12	1-2	1-4	Grass, herbs, low *Rubus* sp.	3-4	Grass, herbs	3-4 1-4	Anything Clumped shrubs
13	1-2	1-4	Grass, herbs, low *Rubus* sp.	3-4	Grass, herbs	1-2	Anything but clumped shrubs
14	1-2	1-4	Grass, herbs, low *Rubus* sp.	3-4 3-4	Single-stemmed shrubs OR *Corylus cornutus*	3-4 1-4 1-4	Anything Clumped shrubs Anything
15	1-2	1-4	Grass, herbs, low *Rubus* sp.	3-4	Clumped shrubs	1-4	Anything
16	1-2	1-4	Grass, herbs, low *Rubus* sp.	3-4	*Rubus* sp. and/or *Rosa* sp.	1-4	Anything
17	1-2	1-4	Grass, herbs, low *Rubus* sp.	3-4	Single-stemmed shrubs	1-2	Anything but clumped shrubs
18	1-2	1-4	Grass, herbs, low *Rubus* sp.	3-4	*Ledum groenlandicum*	1-4	Anything
19	1-2	1-4	Grass, herbs, low *Rubus* sp.	1-2	Anything	3-4 1-4	Anything Clumped shrubs
20	1-2	1-4	Grass, herbs, low *Rubus* sp.	1-2	Anything	1-2	Anything but clumped shrubs
21	3-4	1-4	Grass, herbs, low *Rubus* sp.	3-4 1-4	Anything Clumped shrubs	1-4	Anything
22	3-4	1-4	Grass, herbs, low *Rubus* sp.	1-2	Anything but clumped shrubs	1-2	Anything but clumped shrubs

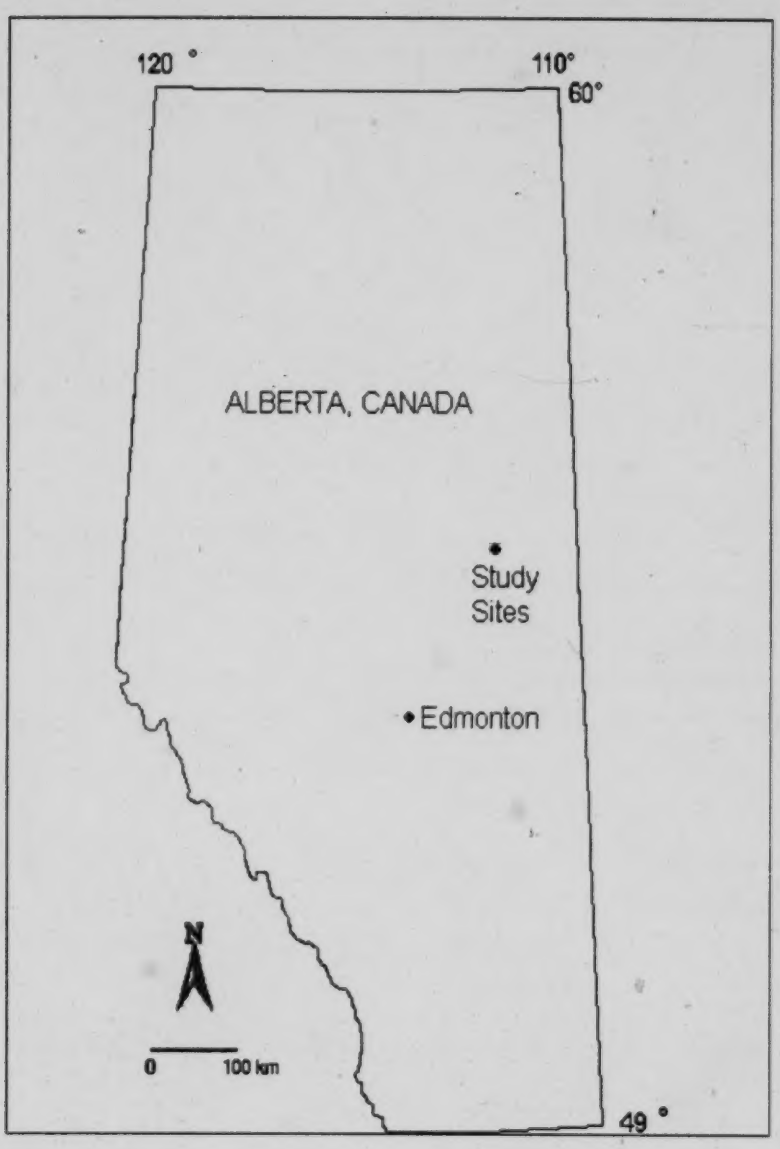


Figure 3-1. Map of Alberta, Canada, indicating the location of study sites about 350 km northeast of the capital city of Edmonton.

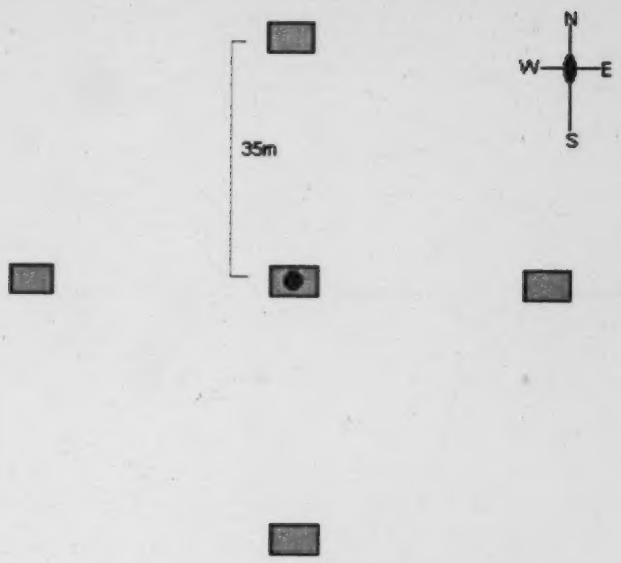


Figure 3-2. Ideal placement of Tin Cat small mammal live traps at a sampling point. Trap locations were flagged to establish permanent trapping stations.

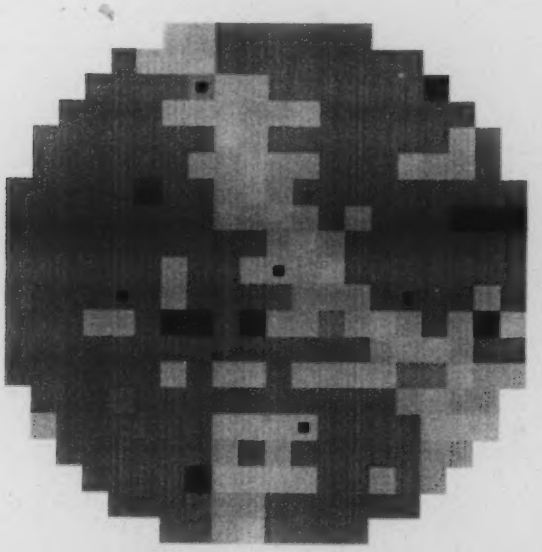


Figure 3-3. An example of an understory vegetation cover map from a mature aspen stand with herbaceous ground cover. Black squares denote permanent live trapping stations. The continuous patches in the southwest and northeast of this map represent beaked hazel, while the band running southeast to northwest indicates a cutline with *Rubus*, *Populus* and grasses.

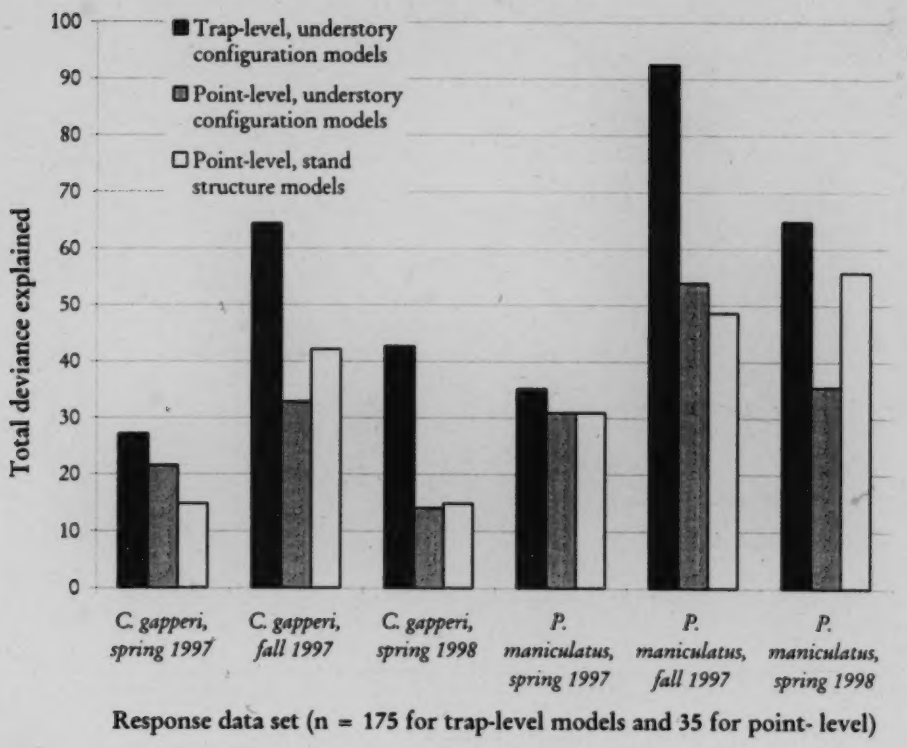


Figure 3-4. Deviance explained by full models for both species. Trap-level models explain the most deviance in all situations, while point-level models are roughly equal, whether analyzed with understory configuration or stand-level landscape structure.

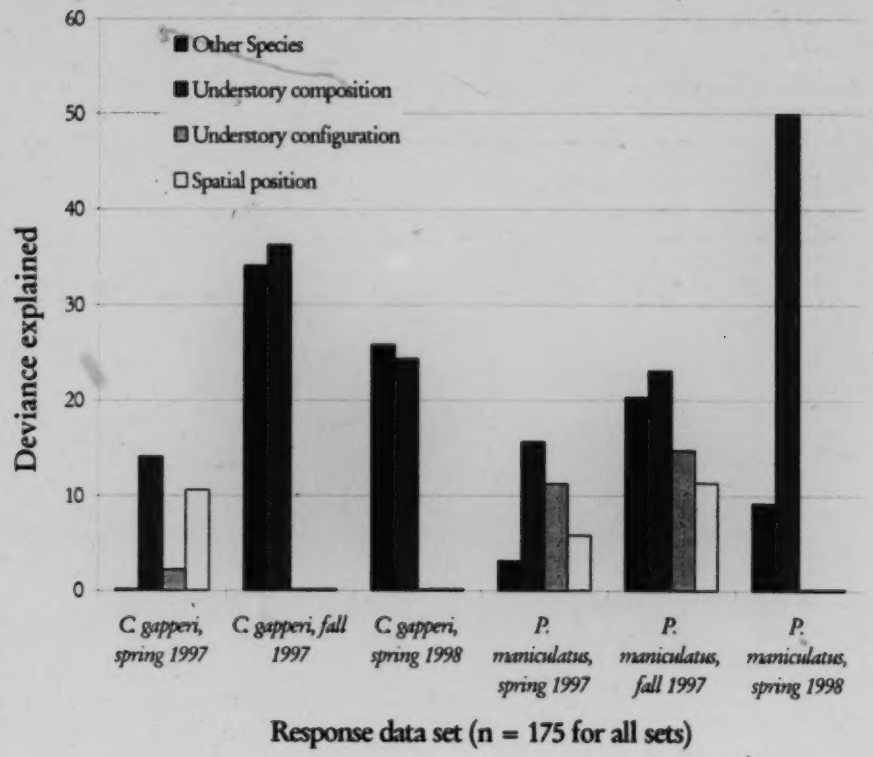
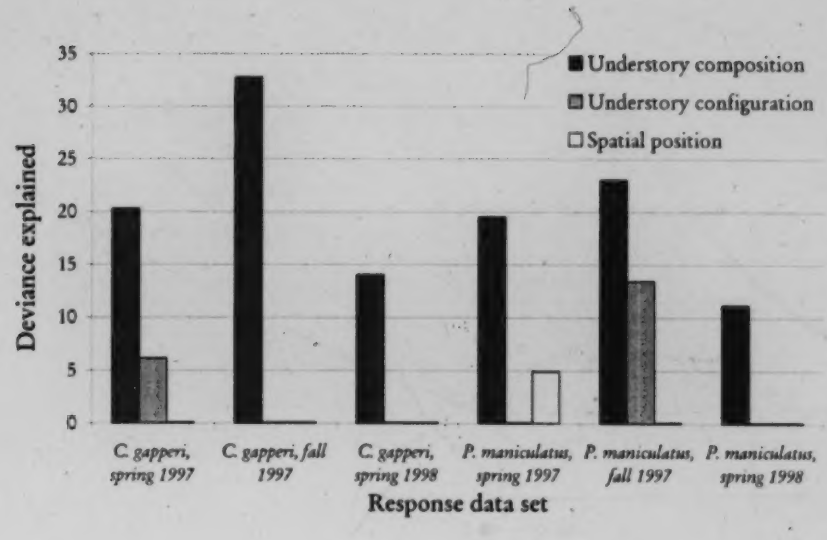


Figure 3-5. Deviance explained by each predictor data set in trap-level models of abundance. Models from both species are presented here. The abundance of the other species at a trap station is the best predictor in most cases, followed by understory landscape composition. Understory configuration and spatial position have little predictive ability for these data sets.

3-6a



3-6b

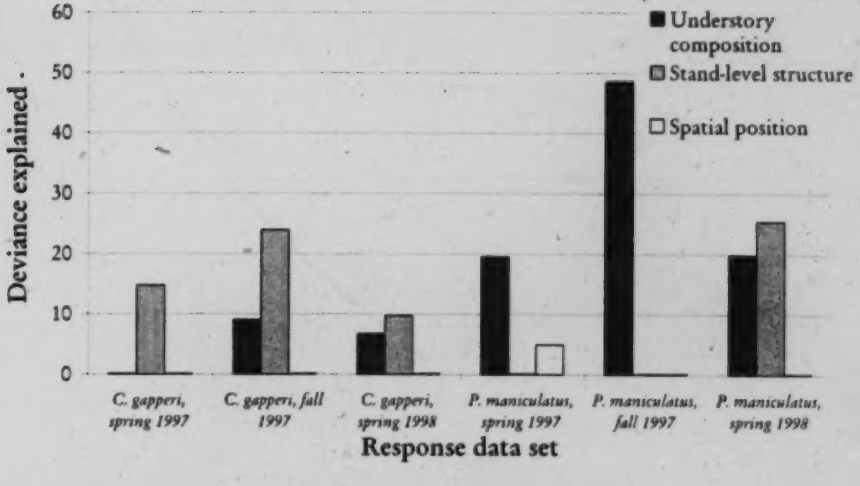


Figure 3-6. Deviance explained by each predictor data set in point-level analyses with understory landscape configuration (a) and forest stand structure (b) as landscape predictors. The distribution of explanatory power changes with the landscape type considered for *C. gapperi*. Understory composition is the main driver when understory configuration is submitted to models, whereas forest stand structure outweighs understory composition when it is submitted. There are no strong patterns of response to the two grains of landscape structure for *P. maniculatus*.

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Chapter 4 - General discussion

This study used a multi-scale approach to investigate landscape effects on small mammals in Alberta's boreal mixed-wood forest. This involved examining different grains and extents of landscapes to see what scale(s) resulted in the best models of abundance. It was discovered in the course of the study that the importance of extent in the measurement of landscape effects might be grain- and species-specific.

Stand-level landscape structure affected both *Clethrionomys gapperi* and *Peromyscus maniculatus*. Landscape composition explained almost as much variation in *C. gapperi* numbers as did local vegetation, and this effect was greatest in the fall and on the managed study area where harvested deciduous stands were common. Composition was also important for predicting *P. maniculatus* abundance (though vegetation was obviously the key factor), explaining the most variation during the fall on the reference study area where conifer stands (poor habitat) occupied more than half of the forest cover. Similarly, landscape configuration was important for explaining *C. gapperi* abundance only during the fall on reference sites where it was positively related to variables measuring landscape heterogeneity. *P. maniculatus* responded little to configuration, though the relationship to heterogeneity was consistently negative on the burned study area where good habitat was rare and dispersed. These patterns suggest that landscape connectivity is important for the spread and persistence of *C. gapperi* populations, whereas source/sink dynamics may be applicable to *P. maniculatus* populations when good habitat is relatively sparse (*i.e.* occupies less than half of the landscape area)

Stand-level landscape effects were present regardless of the spatial extent of the landscapes used to search for relationships. This may have been because landscape structural variables were highly correlated across extents and that variability in response was very high relative to the average amount of deviance explained at each extent. However, with the number of analyses performed in the study (9 for 250 and 500 m radii and 26 for 50 and 100 m radii), it was expected that the appropriate spatial extents could be identified graphically or statistically by comparing average responses. The absence of patterns with respect to extent, despite this replication, suggests that all the extents considered lie within the range of scales of only one landscape process, causing the same effects across scales. A

number of independent results from this study suggest dispersal is the process most likely affected by stand-level landscape structure at extents greater than a 50 m radius.

Small-scale responses to understory landscape structure within 12.5 m of trap stations likely result from home range selection based on requirements for foraging, nesting and predator avoidance. These effects are generally limited by understory landscape composition for both species. However, there is some evidence that *P. maniculatus* favours more homogeneous understory within home ranges, as opposed to diverse, heterogeneous areas.

Comparing understory landscape variables related to abundance at 12.5 and 50-m extents reveals those habitat attributes that are important for foraging or home range establishment versus dispersal or immigration. For *C. gapperi*, dense shrubs and lack of herbs are avoided at small extents, while herbs and simple shrubs are positively associated at a larger extent, perhaps reflective of a stand-level association with harvested patches at this scale. *P. maniculatus* shows associations with more open patches of understory at small scales, but requires dense cover of simple shrubs at larger scales. Despite these patterns in response to understory landscapes, the deviance explained by these models was relatively low. It is possible that the grain of understory mapping was too large or patch types were defined by inappropriate criteria, resulting in an inability to detect strong responses.

When examining landscape effects at two different grains for the same set of 50-m radius landscapes, stand and understory models explained similar amounts of variation in abundance for both species. However, a loss of understory effects for *C. gapperi* when stand-level structure was submitted to models suggests that these understory landscape attributes are merely surrogates for the overall stand characteristics that are responded to during dispersal. It may be that the generalist nature of this species in this region allows response to very broad habitat descriptors during dispersal, and that understory within stand types is not crucial for their use. Stand-level landscape structure was less important relative to understory composition when it was included in models for *P. maniculatus* because this species increased in deciduous forests with dense shrubs, and stand-level maps did not distinguish these forests types from deciduous stands with more open understory.

From the patterns demonstrated by *C. gapperi* and *P. maniculatus* in this study, it is possible to make some predictions about small mammal population response to forest management as timber harvesting becomes more widespread in boreal mixed-wood

landscapes. Both of these small mammals respond positively to forest harvesting at the successional stages of young forests in this study (greater than 5 years old). This positive response occurs at both the stand and landscape levels. For these species, especially *C. gapperi*, densities may be expected to increase in landscapes where aspen harvesting occurs. These effects are purely compositional, however, and little can be said for the effects of harvest configuration over landscapes. Results for *C. gapperi* suggest that configuration may only be important in landscapes where poor habitat (jack pine) is a dominant landscape element. In this case, forest management may benefit *C. gapperi* if harvested patches are scattered throughout the landscape, providing connectivity and source habitat for dispersal. However, this may not be important at peak levels of population densities since low-quality habitat may be used more readily during this phase.

Small mammal response to habitats on the burned study area provides no definite evidence as to whether burned forest is either good or bad habitat for *C. gapperi* or *P. maniculatus*, but that landscapes in general tend to be more heterogeneous in burned than in reference or managed areas. There was weak evidence of this heterogeneity being problematic for *P. maniculatus* because of reduced patch sizes of good habitat (deciduous). This would likely not be a problem if the landscape disturbance were harvesting though, since the harvested forest matrix would continue to provide good habitat, whereas burns apparently have little effect.

Extrapolation of these forest management conclusions to other species is not appropriate unless habitat associations of target species are well understood. However, from the detailed study done here, there is little evidence that landscape configuration of harvesting should be an important consideration during planning. The naturally heterogeneous nature of landscapes in this region may have caused resident species to become adapted to the landscape structural changes associated with increased heterogeneity, so that disturbance has little effect.

Overall it has been shown that, for these species, landscape structure within 50 m or more of sampling points affects local abundance by influencing dispersal. Effects on dispersal are best detected using stand-level landscape structure, but understory vegetation may also reveal relationships if stand-level patches contain variability in understory that animals respond to. Landscapes with very small extents are likely occupied based on their home range quality and habitat patches should be defined by food, cover and nest sites.

Though composition was still important, landscape configuration at these scales had limited utility in explaining variation in small mammal abundance in this study. At this stage, it is not possible to conclude if this lack of response to spatial configuration of understory patches indicates a real lack of an effect or a failure of the design to map understory at an appropriate grain.

Subsequent work should focus on determining what characteristics of a species determine its scale of response to landscape structure. Spatial extent of response seems fairly straightforward from the range used in this study, with response occurring at scales encompassing home range sizes or dispersal distances. However, grain may be more difficult to define. The reasons for differences in effects of heterogeneity at dispersal scales are also unclear, and the ability to make generalizations about these types of responses could be very useful for wildlife and land managers in the future.